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THE ROLE OF SPECIFIC RETINAL CELL TYPES IN VISUAL FOLLOWING RESPONSES IN CHICKS (*GALLUS GALLUS DOMESTICUS*)

Lesley J. Rogers
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ABSTRACT: Deficits in visually guided behavior, particularly the optomotor response, are found to follow treatment of the chicken retina with a range of toxic agonists of glutamate and aspartate receptors. These agonists include kainic acid, quisqualic acid, homocysteic acid and N-methyl D-aspartic acid, given either alone or in combination with chemicals which antagonise some aspects of their neurotoxic actions and so cause cell loss of various degrees of specificity. Glutamate itself, when given at a high dose, causes non-specific lesions of the retina but has less effect on the optomotor response than kainate, which causes loss of a specific class of cells. Using these retinotoxins as tools of varying specificity, it is deduced that loss of the optomotor response, together with other visual impairments, is due to loss of amacrine cells and/or displaced ganglion cells. The paper includes discussion of the cellular and neurochemical organisation of the retina, retinal projections involved in the optokinetic response, as well as a summary of the modes of action of the toxins used.

For many years, there has been speculation about the possible role played by certain retinal cell types in the perception of moving visual stimuli. This speculation has been based on the anatomical arrangement of cell connections in the retina and, somewhat more recently, on evidence gained from electrophysiological recording from the different cell types in the retina. Now an increasing number of toxins which lesion specific neuronal types are becoming available, and their use is not only assisting in the interpretations which can be made from electrophysiological studies, but also providing a new means of investigating whether particular behavioural functions, in terms of the whole animal, can be linked to specific cell types in the retina.

Following the recognition that the amino acids glutamate and aspartate are putative neurotransmitters, particularly in the visual system (Bondy & Purdy, 1977), and that they have both excitatory and toxic actions on nerve cells (Olney, Ho & Rhee, 1971), an increasing number of their analogues have been tested for neuroexcitatory and neurotoxic properties (McGeer, Olney & McGeer, 1978). Kainic acid (KA), a conformationally restricted analogue of glutamate prepared from a marine

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alga, is one to two thousand-fold more potent than glutamate in its neurotoxic action, and it is now widely used as a tool for lesioning in the central nervous system, as it destroys cell bodies in the region of its application and spares axons passing through the region (McGeer et al., 1978). N-methyl D-aspartic acid (NMDA), an analogue of aspartate, and quisqualic acid (QA) are also neurotoxins, to name just two more.

It is generally thought that the neuronal cell death ensues by over-excitement of the cells to the extent that their energy supplies are exhausted. This is the "excitotoxic" hypothesis proposed by Olney (1969), and there is evidence to support it, at least in the case of KA. Although high doses of KA have multiple effects both postsynaptically and presynaptically, the latter affecting neurotransmitter uptake and release, at lower doses the action of KA appears to be confined to a stimulation of postsynaptic receptors (Poli et al., 1985). Neurones with more of this specific receptor-type are therefore more vulnerable to KA, these being neurones normally stimulated by glutamate *in vivo* (i.e. glutamatergic neurones). Other neurones which are stimulated by aspartate are more vulnerable to the toxic actions of NMDA and QA. KA appears to act on a sub-type of glutamate receptors, and NMDA on a sub-type of aspartate receptors. Thus, there are differences in the site and extent of lesions caused by equipotent doses of KA, NMDA and QA, apparently due at least in part to the fact that each is selective for a different sub-type of glutamate or aspartate receptors. In most areas of the brain, however, neural specificity is difficult to determine as loss of specific cell types can not be easily assessed. For this reason, the retina has emerged as the prime site in which to study the specificity and mechanisms of action of neurotoxins. Neurones in the retina are organized into distinct layers and this, together with the presence of certain rather unique morphological characteristics (e.g., ribbon synapses in receptor and bipolar cells) allows identification of specific neurone types.

There are three layers of cell bodies in the retina, the outer nuclear layer (containing the cell bodies of the photoreceptors), the inner nuclear layer (largely comprised of the cell bodies of bipolar cells but also of horizontal cells on its outer aspect and amacrine and displaced ganglion cells on its inner aspect), and the ganglion cell layer on the innermost side of the retina. Between these layers of cell bodies there are two layers comprised of axons and dendrites, the outer plexiform layer (in which connection is made between the photoreceptors and bipolars and horizontal cells) and the inner plexiform layer (in which bipolars, amacrine and ganglion cells interconnect).

When high doses (6,000 nmoles) of glutamate are applied to the retina by injection into the vitreous humour, widespread damage is caused to all layers of the retina (Rogers, Zappia & Ehrlich, 1985), probably reflecting an ubiquitous role for glutamate as a neurotransmit-

ter in the visual system. The organization of the ganglion cells is disrupted and there is a reduction in the thickness of the inner plexiform layer and the inner nuclear layer (Plate 1), this effect being greater in some regions of the retina than in others. Rogers et al. (1985) suggested that the irregular distortion of the retina by such a high dose of glutamate may be due to loss of Muller cells which provide structural support for the retina and have uptake mechanisms for glutamate.

The analogues of glutamate or aspartate cause more specific lesions in the retina, indicating that the action of each is confined to a specific sub-type of receptor (Morgan, 1983; Fagg, 1985). Receptors for KA have been demonstrated to occur on bipolar cells (Morgan & Dvorak, 1984), and toxic effects on these cells are first manifest within 5 min of injection as a swelling of the cytoplasm and a pyknotic appearance of the nuclei (see Figure 1). By 12 h after injection one can see cells which are clearly necrotic (Morgan, 1983) and these later disappear leaving the inner nuclear layer much reduced in thickness (Rogers et al., 1985). The effect of KA appears to be consistent across all regions of the retina.

There is a sub-population of bipolar cells situated on the outer aspect of the inner nuclear layer which is highly susceptible to KA. Administering a dose as low as 5 nmoles KA into the eye of the chicken causes these cells to swell (Sattayasai, Rogers & Ehrlich, 1985; although this paper originally incorrectly characterized these cells as horizontal cells). They appear to be the type I bipolar cells formerly characterized by Yew and Meyer (1975) as morphologically distinct from the other bipolars. Morgan and Millar (1986) suggest that they are possibly off-bipolars.

KA also affects amacrine cells, situated along the inner aspect of the inner nuclear layer. This may, however, be an indirect effect following KA's excitotoxic action on bipolar cells, as the first signs of swelling in amacrine cells is delayed by some 10 min after swelling in bipolars (Morgan, 1983). Also, pre-treatment with diazepam or phenobarbitone protects the amacrine cells, but not the bipolars, from KA toxicity (Di Chiara et al., 1981; Imperato, Porceddu, Morelli, Fossarello & Di Chiara, 1981). In other words, KA may excite bipolars directly which, in turn, excite amacrine cells. The presence of phenobarbitone would suppress this secondary excitation (and therefore toxicity), while diazepam may provide a counteracting inhibitory effect by enhancing GABAergic mechanisms.

There are a variety of amacrine cell types each stimulated by a different neurotransmitter (cholinergic, GABAergic, glycinergic, serotonergic and dopaminergic amacrine cells). The dopaminergic amacrine cells do not receive bipolar cell input and these amacrine cells are largely resistant to KA (Coyle, Biziere & Schwartz, 1978; Morgan, 1983), providing further evidence that KA's effect on amacrine cells is mediated via bipolars. Presumably these dopaminergic amacrine cells are not connected to other

amacrines which are stimulated by bipolars, otherwise one might expect them to be destroyed by indirect activation. The cholinergic amacrines are destroyed by low doses of KA; 8 nmoles per eye has been shown to cause loss of half the cholinergic amacrines in the chicken retina (Morgan, 1983).

In some species the ganglion cells are susceptible to KA, but in the chicken the ganglion cells proper (in the ganglion cell layer) are affected by only very high doses of KA (200 nmoles per eye causes a 40% loss of ganglion cells; Tung, Morgan & Ehrlich, 1987). At doses of KA some ten-fold lower than this it is only the displaced ganglion cells which are destroyed, apparently also an indirect effect via stimulation of bipolars.

The displaced ganglion cells are movement sensitive and directionally selective (Karten, 1979). Their dendritic trees are in close register with the cholinergic amacrines (Morgan, pers. comm.), from which they receive their only input (Morgan, 1983). That is, they have no direct input from bipolars, but may be stimulated via the route, bipolars to cholinergic amacrines to displaced ganglion cells. There is considerable evidence that they drive the optokinetic or optomotor response (Karten, Fite & Brecha, 1977; and see discussion below). In the pigeon, the displaced ganglion cells have been shown to be the only ganglion cells with input to the nucleus of the basal optic root (nBOR), which forms part of the accessory optic system and, via its efferent out-put to the vestibulo-cerebellum and oculomotor nuclear complex, drives to the optokinetic response preferentially in the vertical and torsional directions (Karten, Fite & Brecha, 1977; McKenna & Wallman, 1985a; see Figure 1).

In young chicks the nBOR is involved in the optokinetic response triggered by both vertical and horizontal retinal slip, as shown by a study measuring metabolic activity in nBOR neurones (by their uptake of radioactive 2-deoxyglucose) when the chick is performing vertical or horizontal optokinetic nystagmus (McKenna & Wallman, 1985b). In chickens treatment with KA might, therefore, be expected to eliminate the optomotor response to large field movement in both the horizontal and vertical directions, and possibly also impair detection of other types of moving visual stimuli.

The toxic actions of NMDA and QA, studied in chicken retina, appear to be confined to a direct effect on amacrines (Sattayasai & Ehrlich, 1987; Morgan, 1987), which may also indirectly cause loss of displaced ganglion cells. Bipolar cells are not affected. While QA causes an initial swelling of horizontal cells, as well as the amacrine cells, the former cells appear to recover (Sattayasai & Ehrlich, 1987). Ganglion cells are also transiently affected, but recover. Yazulla and Kleinschmidt (1980) have reported a similar short-term swelling of horizontal cells followed by recovery after KA treatment of the retina in goldfish.

Several sulphur-containing amino acids, such as cysteine and homocysteic acid (HCY), also have neurotoxic properties by acting on glutamate and/or aspartate receptors, but their actions appear to be less specific than those of KA, NMDA or QA.

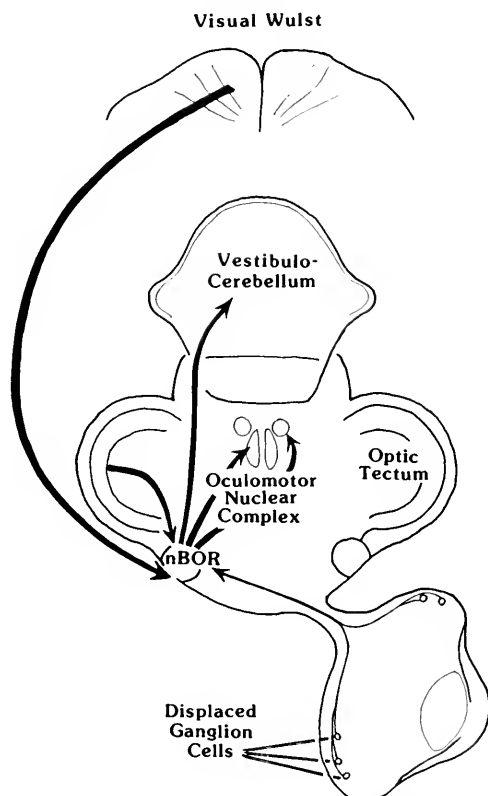


FIGURE 1. Diagrammatic representation of the connections of the nucleus of the basic optic root (nBOR). The nBOR receives inputs from the displaced ganglion cells in the retina of the contralateral eye, the visual Wulst of the forebrain and the optic tectum. Its efferent out-puts go to the vestibulo-cerebellum and the oculomotor nuclear complex.

Despite the now rather considerable amount of anatomical and histochemical research which is investigating the detailed aspects of these retinotoxins, few steps have been made to see how these lesions affect visually guided behaviour. This paper reports some of the first attempts to tie deficits in visually guided behaviour (in particular, the optomotor response) to loss of specific cell types in the retina, the latter being achieved by using a range of toxic agonists of glutamate/aspartate receptors either alone or in combination with other chemicals which antagonise their action.

EXPERIMENT 1

One day old posthatch australorp x leghorn chickens were treated intraocularly with either saline (controls) monosodium L-glutamate, N-methyl D-aspartic acid (NMDA), kainic acid (KA), quisqualic acid (QA) or homocysteic acid (HCY) (all of the acids adjusted to pH 7 with sodium hydroxide). Each drug was administered in a range of doses chosen on the basis of their relative potencies to excite neurones (Watkins, 1978). The doses, expressed in absolute amounts injected, produced responses in the horizontal plane (see below). The saline, 600 to 6,000 nmoles glutamate, 0.6 to 20 nmoles KA, 600 nmoles glutamate, 6,000 nmoles glutamate, 0.6 nmoles KA and 6 nmoles KA NMA, 50 to 1,000 nmoles QA and 50 to 2,000 nmoles HCY. The cgroups were selected for further tests of visually guided behaviour. Controls received 6,000 nmole saline per eye to match the highest dose of drug administered. These were given in a 10:1 volume into the vitreous humour of the chickens, anaesthetised briefly with ether. (N = 6 to 8 per group). Each chick received the same treatment in both eyes.

KA and 6 nmoles KA groups were selected for further tests of visually guided behaviour to ascertain how specific any effects of the treatment conditions on vision might be. On day 10 they were deprived of food for 3 to 4 hours and tested for ability to discriminate food grains from a background of small pebbles of a similar range of colour, shapes and sizes but differing in texture and brightness (for details of method see Rogers, Drennan & Mark, 1974).

Between day 10 and 19 they were tested for ability to detect and peck at a small, red bead (3 mm in diameter) mounted on a rod moved slowly across the floor of the cage. Detection was also scored by moving the bead slowly in a horizontal plane from behind the head towards the beak at a distance of approximately 6 cm from the eye. When the chick detects the bead it gives a startle response, an obvious jerk of the head sometimes accompanied by a trill call (for details see Low, Rogers, Brumley & Ehrlich, 1985). The angle of detection (from the beak) was then estimated for each eye to within the nearest 10°. A mean was calculated from three trials given to each eye.

The experimenter scoring behaviour on the visual tasks was unaware of the drug condition which each animal had received.

The Optomotor Test

The chick was placed in a small glass cylinder centred in the middle of a drum 30 cm in diameter and 68 cm high. The inner wall of the drum

had vertical black and white stripes of 2.5 cm width. It was rotated in an anticlockwise direction at frequency of 0.4 Hz. Tracking ability was assessed by measuring slow, tracking head movements in the direction of rotation of the drum made over two revolutions of the drum and while the chick was standing stationary with its eyes open. This was repeated five times and an average taken.

The optomotor response involves slow tracking movements of the head followed by rapid saccades against the direction of movement of the drum. Only head, and not eye movements were scored, eye movements being minimal in birds. A certain number of random (or, at least, non-tracking) head movements were present in animals which did not show obvious saccades; these were scored when they were in the direction of the drum's rotation, and adherence to this rigid criterion biased the results against finding a visual deficit in the optokinetic response.

The effect of drug treatment was calculated in terms of the difference between the mean number of tracking movements made before treatment and that obtained after treatment. For presentation in the figures the 'optomotor deficit' was calculated as a ratio of this difference of the 'before' minus 'after' score over the score before treatment and expressed over a range with a maximum value of 10 (an optomotor deficit of 10 therefore means complete elimination of the optomotor response).

The raw data were analysed by a one-way analysis of variance followed by a limited number of paired t-tests (one tailed) with degrees of freedom corrected for heterogeneity of variance when a significant ($P < 0.05$) effect of treatment was found.

EXPERIMENT 2

From the data of experiment 1 it was possible to choose (at least within the limits of the doses tested) the lowest dose of each toxin which causes maximal deficits in the optokinetic response. These respective doses of each toxin were then co-administered with 5,000 nmoles magnesium chloride, as Mg^{++} ions antagonise the binding of agonists at NMDA receptors (Watkins, 1981). This antagonism of Mg^{++} at NMDA receptor sites is thought to be due to a reduction in the affinity of the receptors for NMDA (Fain, Ishida & Callery, 1983).

The co-administration of diazepam (1.25 g in 10 l) with 6 nmoles of KA was also tested, on the basis that diazepam blocks the indirect effects of KA and so spares amacrine and displaced ganglion cells (see above).

These chicks were tested for optomotor response only, before and after treatment.

RESULTS

Optomotor Response

As illustrated in Figure 2, treatment with either 600 or 6,000 nmoles of glutamate per eye failed to have any dramatic effect on the optomotor

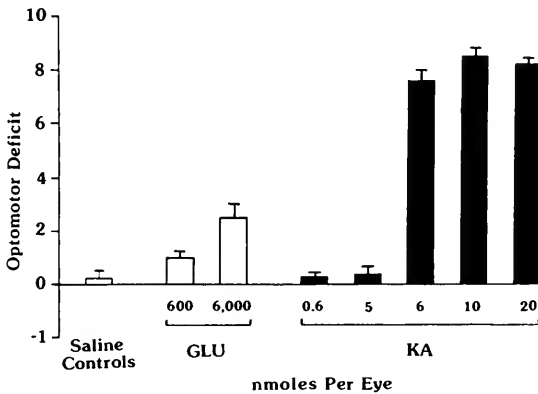


FIGURE 2. Means and standard errors of the deficits in the optomotor responses.

response, whereas a dose of KA as low as 6 nmoles per eye almost completely eliminated the optomotor response ($P < 0.01$; paired t-tests for 'before' versus 'after' treatment scores). Indeed, had a conservative measure of head movements not been adopted, there would have been a total elimination of the optomotor response by 6, 10 or 20 nmoles of KA as no saccades were seen in chicks treated thus. The dose curve for KA is exceptionally steep, 5 nmoles causing no deficit in the optomotor response while 6 nmoles causes a maximal deficit.

It should be noted that two of the 24 chicks treated with 6 or more nmoles of KA appeared to lock on to one set of stripes on the rotating drum and follow this pattern around and around by turning in circles. Occasionally, this whole body movement tracking is seen in controls but in them it rarely lasts for more than one revolution and then the chick stands stationary performing tracking and saccade movements of the head. These KA-treated chicks were unable to stop circling and they never showed the alternate tracking and saccade movement of the head.

As illustrated in Figure 3 the optomotor response is eliminated by NMDA administered in 20 and 50 nmoles doses per eye ($P < 0.05$ for the lower dose and $P < 0.01$ for the higher dose; paired t-tests). The 10 nmoles dose of NMDA caused little effect on the response, suggesting a rather steep dose curve although probably less so than for KA.

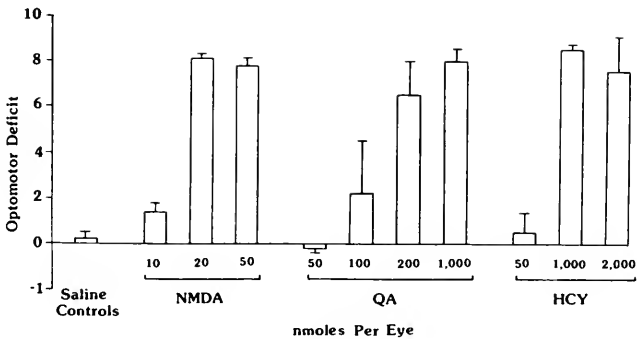


FIGURE 3. Deficits in optomotor responses as a function of drug dose level.

Higher doses of QA were required to cause a significant deficit in the optomotor response (200 and 1,000 nmols QA; for each $P < 0.05$ paired t-tests). The 50 nmole dose of QA had no effect, and the 100 nmole dose caused a deficit in the response of some chicks and not others, as evidenced by the large variability in the mean score ($P < 0.05$ for a Levene's test, showing a significant variance effect).

HCY caused significant deficits in the optomotor response when administered at 1,000 and 2,000 nmols per eye ($P < 0.01$ for each), but not at 50 nmols.

The graded order of potency of these drugs on the optomotor response is therefore $KA > NMDA > QA > HCY$, with glutamate having no marked effects even at exceptionally high doses.

The lowest doses which caused a maximal deficit in the optomotor response (viz. 6 nmol KA, 20 nmols NMDA, 200 nmols QA and 1,000

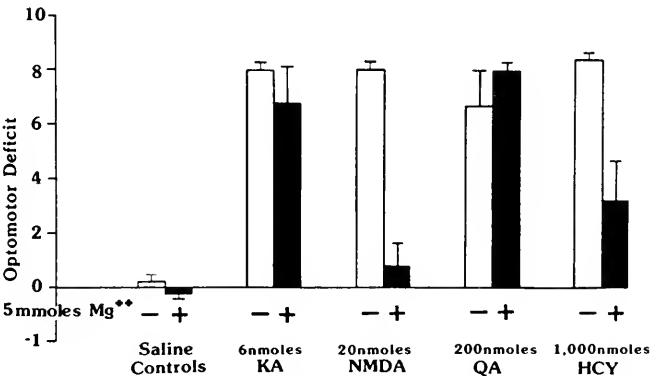


FIGURE 4. Effects of administration of 5 nmole of Mg^{++} on the means and standard errors of optomotor deficits produced by various excitotoxins.

nmoles HCY) were then chosen for co-administration with 5,000 nmoles of Mg^{++} . As seen in Figure 4 the presence of Mg^{++} ions antagonised the effect of NMDA, and to a lesser extent the effect of HCY, but had no effect on the deficits caused by KA and QA.

Co-administration of diazepam with 6 nmoles of KA did, however, reverse the deficit in the optomotor response caused by KA (Fig. 5).

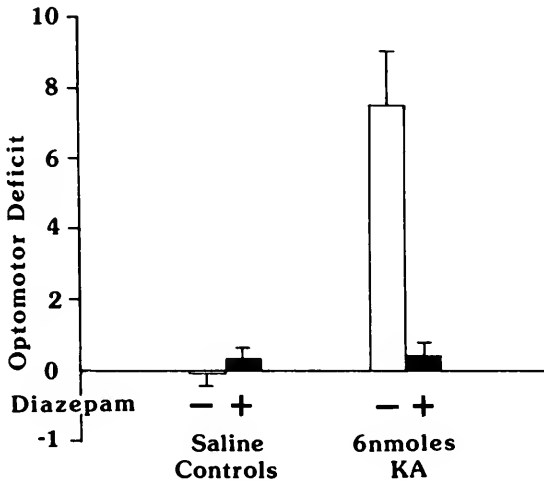


FIGURE 5. Effects of diazepam administration on the toxicity of KA on optomotor responses.

Visual Discrimination Performance

In the last 20 pecks of the task requiring the chicks to discriminate grain from pebbles, the control, saline-treated chicks made a mean of less than one error, errors being pecks at pebbles, whereas those treated with 6,000 nmoles glutamate and 6 nmoles KA failed to discriminate grains from pebbles (Table 1). The 0.6 nmoles KA had no effect on performance in this task and the 600 nmoles glutamate caused only a slight increase in the number of errors.

Detection of a Moving Bead

All of the control chicks detected the moving bead at an angle greater than 100° from the beak (Table 1). In each of the groups treated with 600 nmoles of glutamate or 0.6 nmoles KA there was only one chick which had less ability to detect the bead than did controls. The 6,000 nmoles dose of glutamate had a variable effect: half of this group detected the bead at greater than 100° from the beak, as controls, but the other half either failed to respond or detected it at an angle of less than

TABLE 1
Visual Discrimination Performance

<i>Treatment</i>	<i>Visual Discrimination (Errors in last 20 pecks)</i>	<i>Detection of moving bead</i>	<i>Pecking aim</i>
Saline controls	0.7 (0.4)	> 100°	+
600 nmoles glutamate	3.5 (0.9)	> 100°	+
6,000 nmoles glutamate	10 (±2.4)*	variable (see text)	-
0.6 nmoles KA	1.1 (0.4)	> 100°	+
6 nmoles KA	11 (1.2)*	no response	-

Note: Visual discrimination performance is scored in terms of the number of errors (pecks at pebbles) in the last 20 pecks of the task, given on day 10 (first column). Means (with standard errors) are given. Asterisks indicate a significant difference from controls ($P < .05$; one-tailed t-tests). Detection of a moving bead advanced towards the beak from behind the head in a horizontal plane 6 cm from the eye was scored in terms of the angle from the beak at the point of detection (second column). Pecking aim was scored by moving the same bead at floor level (+ means good aim, - poor aim, often 2 cm out).

30° (i.e. in the binocular field). All of the chicks treated with KA failed to respond to the moving bead by giving a startle response; yet they made vague following movements of the bead when it was moved in the binocular field.

Pecking Aim

The ability to peck at the bead when moved slowly across the floor was grossly impaired in the chicks treated with 6 nmoles KA. None of the latter were able to make beak contact with the stimulus and they often pecked up to 2 cm to one side of it or short of the floor (Table 1). They did, however, attempt to follow and peck at the bead indicating at least partial vision. More than half of the group treated with 6,000 nmoles glutamate had a similar inability to aim. The lower doses did not impair aiming ability.

DISCUSSION

Although the high dose of glutamate (6,000 nmoles) caused poor pecking aim, inability to discriminate grain from pebbles and impaired

ability to detect the moving bead, it did not cause more than a marginal deficit in performance of the optomotor response. Given the patchy distribution of glutamate's effect on the retina, it may be that large field movement, as in the optomotor test, can be detected while small stimuli, moving or not moving, cannot. Using biochemical techniques, Lund Karlsen and Fonnum (1976) have shown that systemic treatment of neonatal rats with glutamate reduces the number of GABAergic and cholinergic neurones in the retina, but this loss may occur in some regions and not others. The results for glutamate are difficult to assess, but it is worth noting that a glutamate-treated retina, which looks more distorted and damaged than a KA treated retina (Plate 1) or, indeed, a NMDA- or QA-treated retina (Sattayasai & Ehrlich, 1987), actually has less functional loss of vision.

KA causes a consistent lesion across the retina and a dose as low as 6 nmoles causes loss of the optomotor response, impaired pecking aim, inability to perform the visual discrimination task and impaired detection of a moving bead. It is interesting to note that 5 nmoles of KA cause swelling of a sub-type of bipolar cells 2 hr after treatment (Plate 1), but this dose does not cause a deficit in the optomotor response. The amacrine and/or displaced ganglion cells must be spared at this dose, possibly because the swelling of this type of bipolars may be transient with later recovery.

The dose curve for KA's effect on the optomotor response is an extremely steep one. Coyle et al. (1978) found a similar steep dose curve

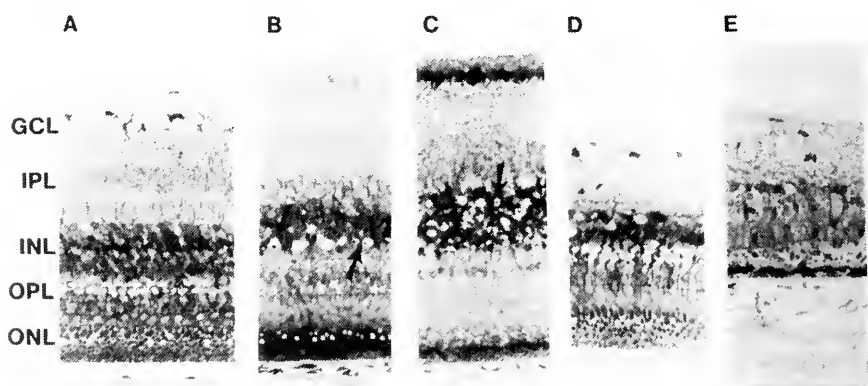


PLATE 1. Light micrographs of chicken retinae. A. Control, saline-treated retina (6,000 nmoles) sampled 10 days after treatment. B. Retina 2 hr after a 5 nmole dose of KA given intraocularly. C. As for B, 2 hr after a 10 nmole dose of KA. D. Retina sampled 10 days after a 6 nmole dose of KA. E. Retina 10 days after a 6,000 nmole dose of glutamate.

Ganglion cell layer (GCL); inner plexiform layer (IPL); inner nuclear layer (INL); outer plexiform layer (OPL); outer nuclear layer, photoreceptors (ONL). The arrows in B and C indicate bipolar cells with swollen cytoplasm and pyknotic nuclei. In D these cells, having been destroyed, are no longer present, and there is a reduction in thickness of the IPL and INL. Note the distortion of all layers in E.

for KA's reduction of activity of the enzyme chlorine acetyl transferase in the retinae of chicks. They found no effect of 5 nmoles KA but a half maximal reduction of enzymic activity with 15 nmoles KA.

The effect of KA on the optomotor response appears to be an indirect one involving amacrine and/or displaced ganglion cells, as co-administration of diazepam protects the chicks from the elimination of the optomotor response caused by KA. It would be interesting to see if diazepam can protect the chicks from the other visual deficits caused by KA.

NMDA affects a different population of receptors than does KA. This has been shown anatomically, and the data reported here illustrate the same phenomenon at a functional level. The Mg^{++} ions block the deficit in the optomotor response caused by NMDA but they afford no protection against the effect of KA. Similarly, Mg^{++} gives no protection from the effect of QA, suggesting that QA also acts at a different receptor sub-type. From previous anatomical studies, the QA receptors are confined to amacrine cells (Sattayasai & Ehrlich, 1987).

HCY appears to have a less specific effect, as Mg^{++} affords some protection from its effect on the optomotor response but the protection is not maximal. HCY is also far less potent in causing a functional deficit in the optomotor response than any of the drugs tested.

Overall, the results implicate a decisive role for amacrine and/or displaced ganglion cells in the horizontal optomotor response. In the chicken, ordinary ganglion cells are not affected by KA, NMDA or, at least permanently, by QA, and co-administration of diazepam with KA protects the amacrine and displaced ganglion cells, but not the bipolar cells. Thus, the bipolars and the ganglion cells proper (in the ganglion cell layer) play no essential role in the optomotor response. Amacrine cells are involved in integration across the retina and for that reason they are thought to have a role in the detection of movement. At least one population of amacrine cells, the cholinergic amacrine, would appear to sustain a role in the optomotor response via their connection to the displaced ganglion cells. As already discussed, the nucleus of the basal optic root (nBOR) receives input from displaced ganglion cells only (as shown in the pigeon) and it is involved in the optokinetic response via its output to the oculomotor nuclear complex and the vestibulo-cerebellum. In the pigeon the nBOR may be mainly involved in the optomotor response to movement in the vertical direction, but in the chicken the nBOR is active when horizontal retina slip occurs (McKenna & Wallman, 1985b). Thus, loss of the horizontal optomotor response after KA, NMDA and QA treatment may result from a specific loss of displaced ganglion cells or, rather, the cholinergic amacrine which feed on to them.

Karten et al., (1977) have suggested that the displaced ganglion cells control the fast (saccadic) phase of the optomotor response. If so, this may explain the performance of the two KA-treated chicks which

appeared to lock on to the moving stripes and follow the rotating pattern around continuously. No suppression of the slow tracking movement to perform a saccadic return of the head, and so track a new set of stripes, may have been possible.

Although lesioning the nBOR has been shown, in the pigeon, to abolish the ability to show optomotor tracking of higher velocity movement in the horizontal direction, the response can still be performed at lower velocities (Fite, 1979). The nBOR is thus not the sole region controlling optokinetic nystagmus. The other central substrate involved is the lentiform nucleus of the mesencephalon, and this is specialised for horizontal retinal slip (McKenna & Wallman, 1985b). It receives input directly from the retina (Ehrlich & Mark, 1984), indirectly from the visual Wulst (Miceli, Gioanni, Repérant & Peyrichoux, 1979) and from the nBOR (Brecha, Karten & Hunt, 1980). Loss of amacrine and/or displaced ganglion cells after treatment with KA, NMDA or QA must eliminate the ability of both the nBOR and the lentiform nucleus to drive the optomotor response. Both systems must, therefore, have the similar requirements of retinal input. It is not known which ganglion cells provide input to lentiform nucleus, but the data reported here may be taken to suggest that, as for the nBOR, the input is from displaced ganglion cells.

The visual Wulst sends efferent projections to the nBOR (Rio, Villalobos, Miceli & Repérant, 1983; see Figure 1) and it may play a role in visual following responses. Indeed, we have recent data showing that there is an increased uptake of 2-deoxyglucose in regions of the visual Wulst in chicks performing the optomotor response (Rogers & Bell, in preparation).

It is unlikely that the deficits in detecting a small moving bead caused by glutamate and KA are due to loss of displaced ganglion cells or any other impairment of input to the accessory optic system. Detection of small moving objects appears to be a property more characteristic of the optic tectum. Although the doses of KA used in these experiments had no observable toxic effect on the ganglion cells which send their axons to the tectum, amacrine cells modulate information transfer between the bipolar and ganglion cells and their loss could affect tectal input from the retina.

The amacrine cells receive efferent input from the isthmo-optic nucleus, and lesions of the isthmo-optic nucleus impair the ability of chickens to detect small moving beads in much the same way as found in these experiments, albeit to a somewhat lesser degree (Rogers & Miles, 1972). Miles (1972) showed that the feed-back loop, retina to tectum to isthmo-optic nucleus and back to amacrine cells of the retina, is important in detection of moving spots as well as moving edges. Isthmo-optic units are particularly responsive to dark edges moving obliquely down across the visual field towards the beak, the passage of which transiently

enhances responsiveness to small moving spots. Miles (1972) suggested that the system may aid visual search into dark areas as when turning the head to search for beetles in shade, and for allowing the animal to deal with the consequences of its own movement. Chicks with lesions of the isthmo-optic nucleus have impaired ability to discriminate grains from pebbles, particularly in areas of low light intensity (Rogers & Miles, 1972). This might suggest that the inability of KA-treated chicks to perform the same visual discrimination task is due to loss of amacrine cells.

Loss of one cell class in the retina, such as the amacrine cells, would, therefore, appear to disrupt visual processing in more than one of the central visual systems and lead to a collection of functional impairments in visually guided behaviour. Specificity at the retinal level does not confer specificity at the functional level, but with the possibility of placing lesions with greater specificity for cell type and sub-type in the retina, and by making comparisons across species, we have the potential to understand more about retinal and central circuitry in the visual system and how this translates into visual performance of the whole animal.

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PATTERN RECOGNITION INVARIANCE IN PIGEONS (*COLUMBA LIVIA*): OUTLINE, COLOR AND CONTRAST

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ABSTRACT: Pigeons that had extensive training with an oddity-from-sample discrimination procedure using visual patterns, and that could transfer their performance to novel patterns, were tested for three kinds of pattern recognition invariance. In one invariance experiment the sample stimuli were silhouette shapes and the comparison stimuli were outline figures. In another experiment the samples were white shapes on a dark background whereas the comparisons were black shapes on a bright background. In a third experiment the sample and comparison shapes were of different color. All the shapes used for invariance testing were novel to the pigeons. Performance during the tests was above 90% correct except in the case of the reversed contrast experiment, where it reached only 77%; dazzling and/or attention problems may have been a disturbing factor. Even in this condition, however, significant transfer was obtained. Generally the pigeons showed that they are capable of invariant shape recognition under all three conditions. Since all critical tests involved shapes that were novel to the subjects the results also confirmed that pigeons can conceptualize a relational oddity/identity rule.

ZUSAMMENFASSUNG: Tauben, die vielseitige Erfahrung mit einer visuellen Wahl-nach-Muster Diskriminationsprozedur hatten und die fähig waren, ihr Wahlverhalten auf neue Formen zu übertragen, wurden mit drei verschiedenen Erkennungsinvarianzaufgaben getestet. In einem Invarianzversuch waren die Musterreize Silhouetten und die Vergleichsmuster Umrisse. In einem anderen Experiment waren die Muster weiße Formen auf schwarzem Hintergrund, während die Vergleichsmuster schwarze Formen auf weißem Hintergrund waren. In einem dritten Experiment waren die Muster- und Vergleichsformen verschiedenerlei Farben. Alle die Formen, die zur Invarianzprüfung benutzt wurden, waren für die Tiere neu. Die Unterscheidungsleistungen lagen bei den Tests über 90% richtige Wahlen außer bei dem Kontrastumkehrungsexperiment, wo sie nur 77% richtige erreichten. Blendungs- oder Aufmerksamkeitsprobleme mögen in diesem Fall beeinträchtigend gewesen sein. Aber selbst bei dieser Bedingung war der Leistungstransfer signifikant. Insgesamt zeigten die Tauben, daß sie unter allen drei Bedingungen der invarianten visuellen Formerkennung fähig sind. Da alle kritischen Tests den Tauben unbekannte Formen beinhalteten, bestätigen die Ergebnisse auch, daß sie fähig sind, eine relationale Gleich-/Verschieden-Regel zu konzeptualisieren.

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On different occasions one and the same object can cast very different images upon the retinae of an observer. The distance and orientation, the prevailing lighting, the viewing conditions generally can drastically modify the image that an object projects on the photo-receptor array. Since object recognition is an essential function of most visual systems central neural processing has to somehow cope with these retinal image vagaries. Such compensation for image variation is said to ensure the invariance of object recognition. Mechanisms that implement invariance may, by extension also play a role in cases where the actual visual properties of objects change inherently (trees in the course of spring for example) or when similar though not identical objects are recognized as belonging to a category (different leaves as oak-leaves for example). In fact, investigations on invariance mostly proceed by examining how well subjects recognize the similarity of patterns actually differing by selected properties.

The invariance competences of humans have been extensively studied from this point of view. Theoretical considerations in connection with artificial vision engineering have suggested that invariance capabilities as a rule require considerable information processing (Hord, 1982). Little is known about the invariance capacities of animals. Even though the behavior of many higher vertebrates in their natural environments suggests that they have comprehensive invariance competences, there have been few studies that show this formally. The abilities of pigeons are of interest in this respect, since as a microcephalic species they must be suspected to be short of sufficient processing capacities to deal with all invariance varieties. Following basic evolutionary arguments it is assumed that small brained organisms have been selected so that whatever capacities they possess have been allocated to ecologically meaningful functions. Extensive studies on visual perception in birds done in our laboratory have been successfully guided by these considerations (Delius and Emmerton, 1978; 1979). Visual pattern recognition invariance results relating to orientation variations (Hollard and Delius, 1982; Delius, 1986; Delius and Hollard, 1987; Lombardi, 1989) and with respect to size variations (Lombardi and Delius, 1989) have already been reported. Here we describe experiments whose primary purpose was to obtain baseline information on the color, outline and contrast invariance capacities of pigeons.

A simultaneous oddity-from-sample conditioning paradigm was used. To simplify technical matters the recognition of two-dimensional patterns rather than three-dimensional objects was studied. During training trials subjects were first shown a sample shape and then presented with two alternative comparison shapes, from which they had to choose the one that was different from the sample and avoid the one that was identical with the sample. Correct choices were rewarded with food. Subsequent transfer trials involved shapes that were novel to the

subjects. Previously it had been demonstrated by us that given propitious training conditions (involving principally the use of many exemplar stimuli), pigeons solved this task by applying a relational oddity/identity concept (Lombardi, Fachinelli and Delius, 1984; Lombardi, Delius and Hollard, 1986). The present experiments as a matter of fact involved several further tests of this ability, a point to which we shall return later. In the invariance test trials that were essential to this study both comparison shapes differed from the sample by a particular feature (color, outline or contrast). The pigeons' problem consisted in nevertheless recognizing the oddity/identity relations between sample and comparison shapes.

EXPERIMENT 1: OUTLINES

Humans can easily recognize objects represented in line drawings, and indeed they are often required to do so in the modern cultural environment. There is obviously no comparable demand in the pigeon's environment. In fact, some experimental evidence seems to indicate that pigeons cannot perceive the correspondence between line drawings and the solid objects they represent (Cabe, 1976; Cabe and Healey, 1979; see also Cerella, 1982 for supporting evidence), although they probably interpret full silhouettes and photographs of objects correctly. Cook, Wright and Kendrick (in press), who trained pigeons to distinguish between naturalistic drawings of mammals and birds found no transfer to mere outline drawings, although there was some transfer to silhouette representations. Towe (1954) reported a single test where pigeons that had previously learned to discriminate a silhouette triangle from a silhouette square also distinguished between an outline triangle and an outline square.

The present experiment sought to settle the elementary question whether pigeons recognize the shape identity/oddity between silhouette (surface) and outline (perimeter) patterns using more complex and varied shapes. The more general question whether pigeons recognize the equivalence of pictures and objects has been addressed in another study (Delius, 1989; see also Lumsden, 1977).

Method

Animals. Nine adult homing pigeons (*Columba livia*) of local origin were used. They were housed in individual cages located in a well-ventilated room, kept at 18°C, with a 14-h light, 10-h dark cycle. The birds were maintained at 85% of their normal weights throughout the experiment. They had previously served in other experiments involving oddity concept learning and size invariance tasks (Lombardi, Fachinelli and Delius, 1984; Lombardi and Delius, 1989).

Apparatus. A three-key Skinner box of conventional design was employed. The response keys were 7 cm apart and 20 cm above the floor. The food hopper was located below the central key 7 cm above the floor. The stimuli were back-projected onto the response keys with the aid of an automatic projector. Three electromagnetic shutters placed directly behind the keys controlled the displays on these. The projector was equipped with photocells that sensed the presence or absence of coding perforations in specially made slide frames. The decorative geometric patterns used as stimuli were selected from among a large collection routinely used in our laboratory. They were originally drawn in black ink on white paper. Photographically reduced negatives were affixed to the slide frames. The shapes, one to a key, appeared as white patterns of about 10x10mm on the dark background of the 25mm diameter keys. The pattern shown on the central key served as the sample, those shown on the side keys served as comparison stimuli. On each trial, one of the comparison stimuli was identical or equivalent to the sample, the other was different. Such three-stimulus constellations will be called sets. Given n number of different patterns there are $m = 2n(n-1)$ possible sets when odd pattern to the right and odd pattern to the left constellations are included. In some instances (specified below) a random selection from among such a collection of sets was made to keep their number manageable. Care was taken that if the odd-right version of a combination was used, the odd-left version was also used. A microcomputer controlled all events within the experimental sessions, and the relevant performance data were recorded on a trial by trial basis.

Training Procedure. As explained above all the subjects had had extensive experience with the oddity-from-sample task, so no shaping or pretraining was necessary. The subjects were simply retrained for 4 sessions. Each trial within these sessions began with a pattern, the sample stimulus, being projected on the middle key. As soon as the subject pecked this key 15 times, the two comparison stimuli were additionally and separately projected on the two side keys. One comparison pattern was identical to, and the other was different from the sample displayed on the middle key. When the animal issued 5 consecutive pecks to the key bearing the odd pattern, the stimuli on all three keys were obscured, a reinforcement light came on and grain was offered for 3 sec. When the subject pecked 5 consecutive times on the key bearing the identical pattern, it was punished with a 3-sec time-out during which all the stimuli and the houselight, otherwise on throughout the session, extinguished. Any response pattern other than 5 consecutive pecks on a side key had no scheduled consequences. The time that elapsed between the onset of the comparison stimuli and the first response to a side key was recorded as reaction time. The next trial began 8 sec after the end of reinforcement or blackout. If the subject had responded incorrectly in

the last trial, the new trial was a simple repetition, a correction trial in which the same patterns were presented on the same keys. If the pigeon had responded correctly during the last trial, a new stimulus set was shown in the next trial. Correction trials were discontinued after the penultimate retraining session. At the same time, a partial reinforcement contingency was put into force, such that only 60% of randomly selected trials ended with reinforcement or blackout, the others leading directly into the intertrial interval. These extinction trials (neither food reward nor time out) were inserted to accustom the pigeons to the non-reinforced transfer trials that were essential during the test phase (see below). A session involved the presentation of 40 stimulus sets. These were chosen randomly among the group of sets in use, with the restriction that the position of the odd pattern on the left or right side key was determined by a quasi-random sequence (Fellows, 1967). Only the outcomes of noncorrection trials were used for performance evaluation. Sessions were run daily.

Training Stimuli. Each training session involved the presentation of 24 silhouette sets and 16 outline sets, randomly ordered. The former sets were randomly selected from those that could be assembled with the 15 silhouette (filled) training shapes shown in Figure 1. The birds had already had extensive training with these stimuli in the course of the previous experiments. The outline (perimeter) sets were randomly selected from all those that could be assembled from outline versions of 5 shapes that were novel to the birds (Fig. 1). The outline component was

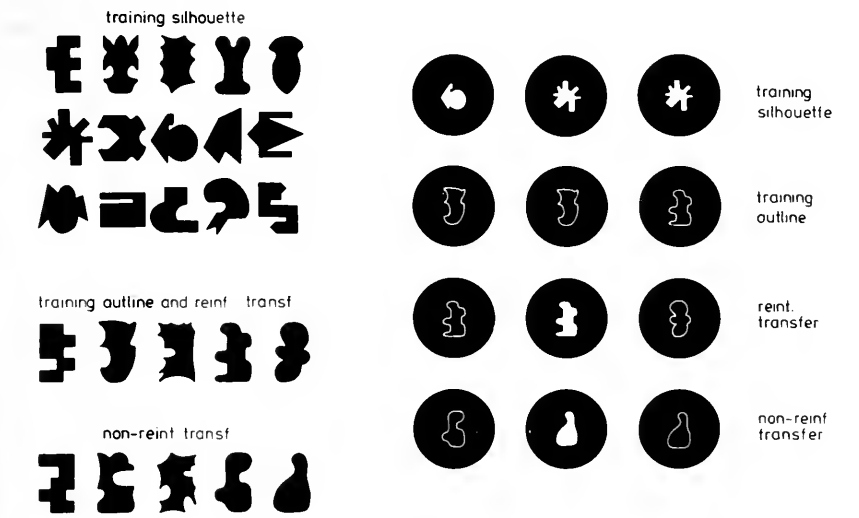


FIGURE 1. Experiment 1: Outlines. Left: all patterns used shown as positives. Right: some examples of the actual stimulus sets derived from the patterns shown left. Dimensions not to scale.

intended to familiarize the pigeons with the altered style of shapes that would be needed during the testing phase.

Testing. Ten transfer sessions followed. Each session consisted of 24 training trials, 16 with silhouette sets and 8 with outline sets selected from among those used in the previous phase, and 16 transfer trials. Eight of these trials involved sets where the sample was always a silhouette and the comparisons were always outline shapes. The outline shapes were already known to the subjects from the preceding phase. The 5 basic patterns yielded 40 sets. All trials involving these sets were reinforced and served to prevent the birds associating mixed silhouette/outline sets with non-reinforcement. The other 8 transfer trials involved sets analogously assembled from silhouette and outline versions of 5 patterns that were completely novel to the birds (Fig. 1). Each of the 40 sets was used twice during the 10 transfer sessions. These invariance test trials were never reinforced. Non-reinforced transfer trials were not given among the first and last 3 trials of a session, otherwise the various kinds of trials were randomly ordered.

Results

Figure 2 shows the mean percent correct trials computed separately for the various components, plotted session by session. Performance on the silhouette sets was high from the beginning onwards. As explained before the subjects had extensive experience with this basic task. Performance on the outline sets was only slightly worse, even though it was the first time that the pigeons were faced with outline shapes. During the initial 4 sessions, however, the mean response latency was significantly longer during outline trials than during silhouette trials (1.01 sec versus 0.76 sec, Wilcoxon test, $p < 0.01$).

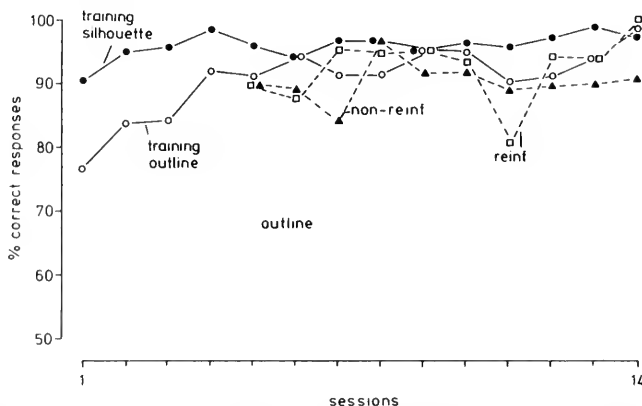


FIGURE 2. Experiment 1: Outlines. Pigeons' performance on the habituation and test sessions. Filled triangles: invariance tests.

The average performance during the reinforced transfer trials involving shapes known to the subjects was 94.1%. The performance on the critical invariance tests (novel shapes, no reinforcement) in which the subjects had to spontaneously recognize the identity/oddity relation between silhouette samples and outline comparison shapes (Fig. 2, filled triangles) was overall 93.8% correct and well above chance for each of the subjects (binomial tests, all $p < 0.01$) and was not significantly worse than that on the reinforced transfer component. The mean response latencies on the various components of the test block rose from silhouette training (0.76 sec) over outline training (0.98 sec) to novel mixed trials (1.13 sec; Friedman analysis of variance, $p < 0.01$).

Discussion

Excellent invariance performance was obtained in this experiment. The recognition of outline comparison shapes as being the "same" as or "different" from silhouette samples was close to perfect; this, even though the shapes used for the critical tests were absolutely new to the birds and never reinforced.

As pointed out previously, in a natural environment it is unlikely that recognition of the correspondence between silhouettes and outlines of shapes is often called for. Only under very exceptional rear lighting conditions can some objects be seen only by their outline halos. It is thus remarkable that pigeons should have evinced such a good performance in our tests. However, theoretical considerations about the processes that subserve pattern recognition (e.g. Marr, 1982) as well as empirical experience with artificial visual systems (e.g. Braddick and Sleight, 1983) suggest that extraction of outline information is generally an efficient initial processing step. It reduces the redundancy of pictorial information without appreciable loss of information essential for later recognition step. Several procedures have been developed to implement outline extraction in artificial systems. A conceptually simple one involves spatial filtering with a particular subset of so-called Laplace operators (Braddick and Sleight, 1983).

Similarly, a certain class of neurons in the visual cortex of mammals seems to be specially engaged in extracting outline information (Creutzfeld and Nothdurft, 1978). It may well be that any visual system that is reasonably efficient in pattern recognition has to incorporate an outline detecting stage. When such a visual system is presented with actual outline patterns (line drawings in the case of humans) these will represent optimal stimuli for this stage, initiating the pattern recognition process. The avian visual system may well conform to this physiological principle even though it is anatomically quite distinct from the mammalian visual system (Emmerton, 1983a; 1983b). Thus the unproblematic recognition of shapes by their outlines found in pigeons and indeed in

humans may not represent an adaptation to a direct environmental demand, so much as an evolutionary by-product of an efficient object recognition strategy.

EXPERIMENT 2: COLORS

The physical color of given objects varies greatly in nature. In accordance with this ecological fact humans by and large have no difficulties in recognizing shapes as being the same regardless of mismatching coloration. In agreement with this, there is much psychophysical and neurophysiological evidence that in the primate brain shape and color information is processed largely independently and that object recognition is primarily mediated by achromatic mechanisms (Livingston and Hubel, 1988). Bird vision may again be functionally similarly organized despite fundamental structural differences (Emmerton, 1983a; 1983b). This leads to the expectancy that the color invariance competences of pigeons should be good. This species is however known to be markedly more responsive to color cues than to shape cues when these compete for attention in the context of discrimination learning (Nelson and Wassermann, 1981; Lombardi and Delius, in preparation; pigeon color vision incidentally is more complex than human color vision: Emmerton, 1983b). Distracting colors could thus after all be expected to disrupt shape oddity recognition. In the critical transfer trials of the following experiment both comparison stimuli were odd with respect to the sample in terms of color but naturally not in terms of shape. The experiment incorporated two consecutive phases: a first one involving one additional distractor color and a second one involving four such colors.

Method

Animals and apparatus. The animals, the general conditions under which the experiment was run and the apparatus were the same as in the previous experiment, except that different stimulus sets were used.

Training. The training of both phases consisted of 6 sessions involving two types of trials. There were 24 white silhouette trials equivalent to those of the training period of Expt. 1, and 16 colored silhouette trials, involving stimulus sets made from 5 patterns already known to the pigeons. For the first phase each of these sets was backed with a piece of red transparent cellophane sheet so that all three shapes of a set appeared as red patterns on a dark background (Fig. 3). For the second phase each of the equivalent sets was backed with either red, blue, green or yellow cellophane. These colored training sets were intercalated at

random among the white training sets. The first three sessions of each training session were run with a correction procedure and continuous reinforcement. The remaining sessions were run without a correction procedure but with the partial reinforcement schedule described above.

Testing. Each phase ended with 10 transfer sessions, each of the sessions consisting of 4 components. There were 16 white and 8 colored training trials as well as two transfer components, each consisting of 8 trials. The trials of one of these components were reinforced; the trials of the other component, the critical invariance tests, were run under extinction conditions. Each transfer component involved 40 sets assembled from 5 patterns. All 20 patterns, 10 for each experimental phase were novel to the birds (Figure 3). Sets corresponding to each phase were each shown twice in the course of the appropriate 10 sessions. The corresponding trials were randomly intercalated among the training trials, avoiding the first and last 3 trials of a session.

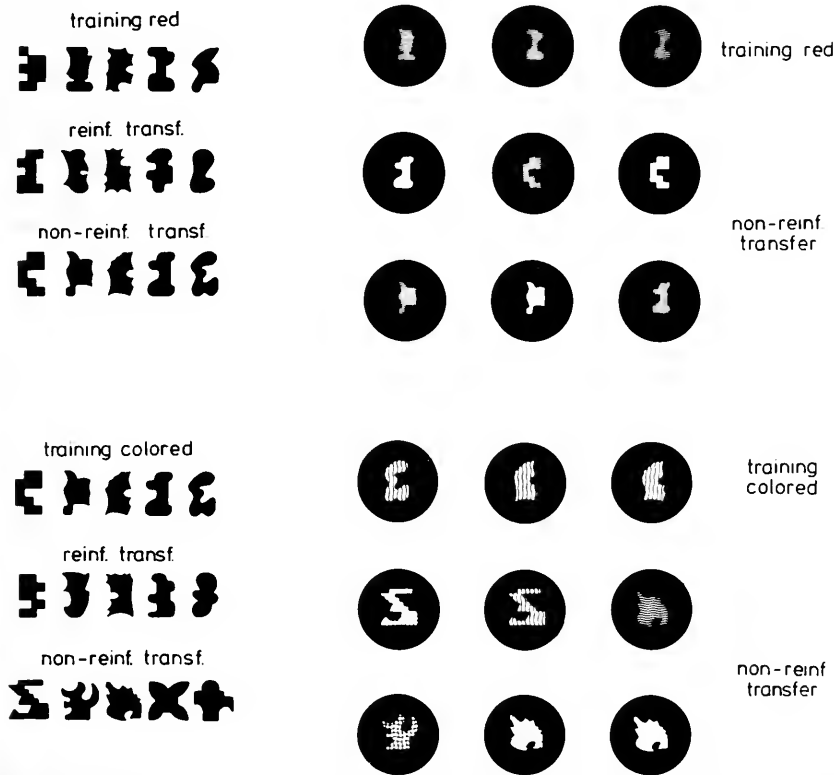


FIGURE 3. Experiment 2: Colors. Left: all patterns (shown as negatives) used in phase I (top) and phase II (bottom). Right: some examples of the actual stimulus sets (shadings indicate different colors, see text) used in the same experiment.

During Phase I, half of the transfer stimulus sets had a red sample pattern and white comparison patterns. Each pattern appeared equally often as a red sample, as a white same comparison and as a white odd comparison. In the same way, the other half of the stimulus sets had white sample patterns and red comparisons. In all cases the background to the patterns was dark (Figure 3). Within each group of transfer trials (reinforced and non-reinforced), four trials per session involved sets with red samples, and four sets with red comparisons. During Phase II each component stimulus of any given transfer set was backed with a different colored sheet of cellophane. Each of the 5 colors (red, green, yellow, blue and white) was equally often attached to sample, to odd and to matching patterns.

Results

The average percent correct performance on the various components of both phases of the experiment is shown in Figure 4 (top). Performance on the white training sets during the first phase was nearly perfect. Performance on the red sets was only slightly poorer. The accuracy on the mixed shade transfer sets was also excellent. In particular, the correct choices on the non-reinforced test trials (overall 95.1% correct) were significantly above chance for each subject (binomial tests, all $p < 0.01$). Differences in performance relating to the red sample/white comparison and the white sample/red comparison sets were not apparent (Wilcoxon test, $p > 0.05$). As in the previous experiment the choice

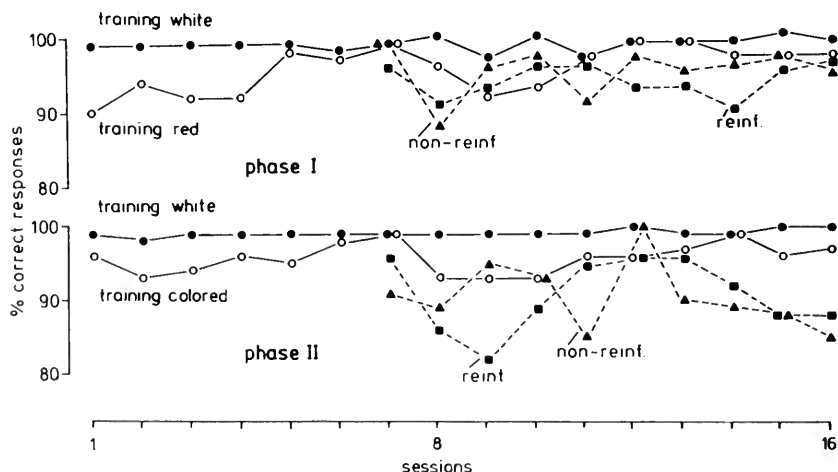


FIGURE 4. Experiment 2: Colors. Pigeons' performance on the habituation and transfer trials of phase I (top) and phase II (bottom). Filled triangles: invariance tests.

latencies rose slightly with presumed task difficulty. The mean reaction times corresponding to white training, red training and mixed non-reinforced test trials were 0.75, 0.86 and 0.90 sec (Friedman analyses of variance, $p < 0.05$).

During the second phase performance on all components was nearly perfect (Figure 4 bottom). The accuracy on the non-reinforced component of the transfer block, the true invariance test, was well above chance (binomial tests, each subject, $p < 0.01$; overall 90.4% correct). As before, though, response latencies increased with presumed task difficulty. The mean reaction times were 0.70, 0.79 and 1.62 sec for white training, colored training and mixed non-reinforced transfer trials respectively (Friedman analysis of variance, $p < 0.1$).

For phase II the effect of the different colors on performance was separately analysed. As regards the colored set trials of the training block, it was found that sets involving red patterns yielded the best performance (98.2% correct) and sets involving yellow the worst (93.3% correct), the other colors being intermediate (Friedman analysis of variance, $p = 0.05$). The data from the colored training trials during the test phase showed the same trend but the differences were not significant (the animals made few errors). Since red was the color used in the previous phase, it is possible that the better performance with red sets was due to greater familiarity with this shade. Analysis of the transfer data helped to clarify this issue, since the sets used there also included white as a shade. White was at least as well known to the pigeons as red, since all the pigeons' experience before Expt. 2 was exclusively with white shapes. Within the reinforced transfer component, the sets with the odd comparison colored red yielded the best performance (93.2% correct) and those with yellow and white odd comparison stimuli the worst (76.6 and 64.1% correct) (Friedman analyses of variance, $p < 0.02$). Within the non-reinforced transfer component an equivalent trend was apparent but it did not reach significance ($p > 0.05$). A similar analysis was done for the colors of the sample patterns and the matching comparison patterns, but no significant differences were found.

Discussion

In accordance with the ecologically based expectation and in disagreement with the distraction hypotheses the subjects showed excellent color invariance. That was so when only 2 (phase I) or as many as 5 (phase II) different distractor colors were involved. Pattern identity/oddity recognition was invariant with respect to color differences. This fits in with the fact that in nature the color of objects is subject to great variation due to both frequent natural variations of the chromatic composition of the illuminating light, but also because equivalent objects

often vary considerably in chromatic reflectance characteristics (maize grains for example) while retaining reasonable shape constancy.

Pigeons are known to have strong spontaneous color preferences (Deliuss, 1968; Sahgal and Iversen, 1975). The expectancy that these would influence the choice behavior during the present experiment was not supported, however. The results of the corresponding analysis are not consistent with a preference for the blue end and an avoidance of the red end of the spectrum reported in the above-mentioned studies. No simple explanation seems to cope with the differential effects that the various distractor colors had on the invariance test performance.

EXPERIMENT 3: REVERSED CONTRAST

The identification of the correspondence/non-correspondence between simple patterns such as letters of opposite contrast mostly presents little difficulty for humans. The task arises very frequently in their culturally determined environment. However, when complex patterns are involved (photographic positives and negatives of portraits for example), humans have considerable problems. Pigeons are undoubtedly rarely confronted in nature with having to recognize the equivalence of shapes in reverse contrast versions. On the other hand, the hypothesis presented earlier that any efficient visual system has to incorporate an outline extraction stage implies proficient reversed contrast invariance. The corresponding filters commonly operate regardless of the contrast sign of edges. Indeed, Towe (1954) has reported briefly that pigeons trained to discriminate a black triangle from a black square on a white background transferred well in a single test to a white triangle and a white square on a black background. The present experiment was designed to check the generality of this finding.

Method

Animals and Apparatus. They were the same as those employed in the previous experiments. Since a pilot experiment had suggested that pigeons have difficulties with discriminating dark patterns on a white background if the overall luminance is too high, a neutral density filter of approximately 1 log unit attenuation was inserted into the optical path of the projector.

Training. The training lasted for 27 sessions. Each session included 24 trials involving the usual white shape/dark background sets. The remaining 16 trials involved black shape/light background sets made up from 5 patterns already known to the subjects (as white shapes; Fig. 5). The first 14 sessions were run with a correction procedure, the

remaining, without. The last three sessions were conducted with the usual partial reinforcement schedule.

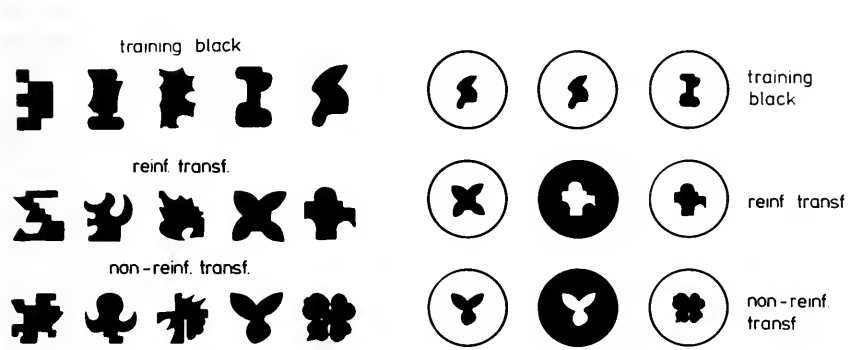


FIGURE 5. Experiment 3: Reversed Contrast. Left: all stimulus patterns. Right: some examples of actual stimulus sets.

Testing. Testing consisted of 10 transfer sessions structured in the same manner as in the previous experiments. In each session there were 16 training trials using white stimulus sets and 8 such trials using black stimulus sets. The remainder of the session consisted of 16 transfer trials (8 reinforced, 8 non-reinforced), using sets that had a white shape as sample, and black shapes as comparisons (Figure 5). The reinforced transfer trials involved 40 sets assembled from 5 shapes known to the pigeons from the test component of the previous experiment. The non-reinforced, invariance test trials involved 40 sets made up from 5 novel patterns, each shown twice within the 10 transfer sessions.

Results

Four pigeons consistently achieved 80% correct responses on the reversed contrast component during the last 10 sessions of the training phase. The other five pigeons that did not achieve that criterion (their performance hovered on the 65% correct mark) did not participate in the transfer sessions.

Figure 6 shows the mean correct responses of the four successful pigeons in the first three and the last three sessions of the training phase, and all transfer sessions. The percent correct choices is shown separately for reinforced and non-reinforced mixed contrast transfer trials. With 77.3% correct choices overall, the performance on the latter, the true tests, was well above the 50% chance level (binomial tests, each animal, $p < 0.01$) but it was markedly worse than on the training and habituation trials. Choice accuracy during the white training, black training and mixed non-reinforced test trials differed significantly (Friedman analysis

of variance, $p < 0.01$). As in previous experiments, the mean reaction times tended to be longer with increasing task difficulty, though the effect was not significant in this case (0.65, 0.88 and 0.94 for training, habituation and non-reinforced test trials respectively; Friedman analysis of variance, $p > 0.05$.)

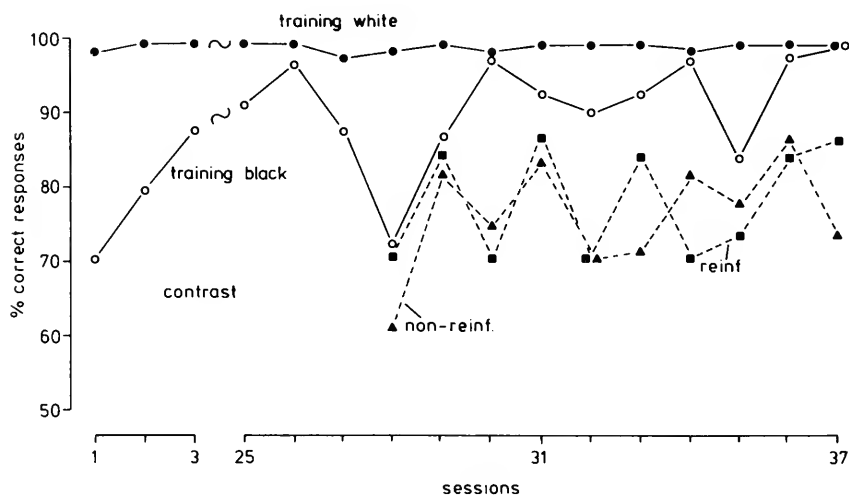


FIGURE 6. Experiment 3: Reversed Contrast. Pigeons' performance on the first three and last three sessions of the training period and all transfer sessions. Filled triangles: invariance tests.

Discussion

Even though the test performance of the 4 subjects that completed the experiment was well above chance, it was comparatively poor. This could be seen as fitting the ecological fact that there is little demand for recognition of objects in reversed contrast versions. It is not certain however that the results necessarily reflect poor pattern recognition invariance in the context of reversed contrast. Five of the 9 pigeons had already experienced considerable difficulty with the reversed contrast training component that did not demand any invariance. An earlier experiment (Lombardi, Delius and Hollard, 1986) had indicated that pigeons can have difficulties with discriminating such dark pattern/white background stimuli due to their higher luminance. Accordingly the present experiment had incorporated a filter to minimize dazzling by such stimuli. It is possible though that the light attenuation was not sufficient.

It could also be that dazzling was not the only reason for poor performance. In a recent, as yet unpublished pattern discrimination experiment pigeons learned with about equal ease to distinguish photographic negative and positive versions of shapes without any brightness adjustments but still had marked problems with transfer between them. In this experiment some incidental evidence indicated that the problem is one of attention. Having extensive training with shapes of one kind of contrast seems to make pigeons reluctant to attend to shapes of the other contrast, perhaps even enticing them to attend preferentially to the irrelevant background of the transfer stimuli. However that may be, Cabe and Healey (1979) contrary to Towe (1954), have also reported that switching from a dark to a light background disrupts the object recognition performance of pigeons. Attempts to investigate why reversed contrast patterns created problems in the present experiment were inhibited by the fact that the pigeons subsequently performed poorly even with normal white shape/dark background training sets. Regardless of what a more successful analysis might have revealed, it is interesting to note that after informal tests human observers also reported that the reversed contrast invariance task was definitely more difficult than either the outline or the color task of the previous experiments.

GENERAL DISCUSSION

The results extend the list of pattern recognition invariance capacities of pigeons. In previous publications we have shown that these animals exhibit an excellent orientation invariance (under certain circumstances even better than humans: Hollard and Delius, 1982; Delius and Hollard, 1987; Lombardi, 1989; see also Emmerton, 1986) and a somewhat more restricted size invariance (Lombardi and Delius, 1989). The considerable invariance competences of pigeons are remarkable in view of their relative microcephaly (their brain is only 2 ml in volume) and the significant information processing known to be associated with invariance implementing algorithms (Hord, 1982).

One of the invariances demonstrated by the present experiments, recognition of shapes regardless of their coloration, matches the ecological situation, since equivalent objects often occur with varying coloration. In humans some of the natural color variations, namely those due to varying chromaticities of illuminants, are taken care of by the phenomenon of color constancy. It reflects a process by which overall chromaticity biases of a scene are centrally compensated before subjective colors are ascribed to individual items. Color constancy has been shown to also operate in goldfish (Ingle, 1985). Our experiments do not yield information on this issue, since what was varied was the pattern's

own colors. Our results do suggest however, that as in primates (Livingston and Hubel, 1988), shape recognition in pigeons is mediated by achromatic mechanisms. A final decision on this point nevertheless will have to await tests with colored shapes whose background is precisely matched for pigeon-subjective brightness.

The partial reverse contrast invariance that was demonstrated can not be easily related to environmental demands. Objects only very occasionally present themselves in reverse contrast as a consequence of special lighting conditions. It may thus not be surprising that the performance of our pigeons on this task was relatively weak. On the other hand, as discussed earlier, this weakness can not be easily accommodated with the birds' good performances on the outline task. Further work will have to examine whether the poor performance with reverse contrast was due to either the very particular conditions of the experiment or a limitation of the pigeons' visual system.

Outline invariance is even less likely than reversed contrast invariance to be ecologically relevant for pigeons. In this kind of task however our pigeons showed excellent performance. To the present results those of another, smaller scale, experiment reported by Lombardi, Delius and Hollard (1986) can be added. There two pigeons showed analogous and significant transfer in tests where they had to detect the similarity/oddity relationship between light silhouette shapes on dark background with dark outline shapes on a light background. This competence is likely to be a by-product of information processing strategies that are efficient for pattern recognition, and include a stage that derives information equivalent to a line drawing. However that maybe, as far as the evidence goes, pigeons appear to command similar invariance capabilities as humans even though they have a visual system of a very different phyletic provenance. Convergent evolution seems to have been at work.

It could be argued that the invariance capabilities we have studied are nothing else than evidence of classical stimulus generalization (Rilling, 1977). Although in a general way it may be reasonable to class invariance as a generalization phenomenon, Lombardi and Delius (in press) have adduced arguments why such allocation may be misleading if it is also meant as an explanation. Briefly, the pigeons in our experiments applied the invariance routine to novel stimuli with which they had no conditioning experience. Stimulus generalization gradients are however conventionally viewed as being coupled to previously conditioned stimuli. Stimulus generalization theory furthermore does not specifically address the situation whereas in our experiments, the discrimination of stimuli differing in one dimension (shape in our case) is still performed by the subjects as the stimuli are modified along other dimensions (color, outline, contrast in our case). To cope with the findings described here stimulus generalization theory at the very least, would seem to require major modifications. It is regrettably true though

that it is not easy at present to offer a new theoretical framework that could take its place.

Indirectly this also bears on the question of whether the invariance capabilities demonstrated with the oddity-from-sample paradigm would also automatically emerge with other discrimination paradigms. Lombardi and Delius (in press) have argued and Lohmann, Delius, Hollard and Friesel (1988) have demonstrated specifically with respect to orientation invariance that this is not necessarily so. Invariance of shape recognition is known to be a facultative option in humans, and the situation cannot *a priori* be expected to be different in pigeons. In fact, Pepperberg (1987) has shown that at least one individual of another avian species (African grey parrot) can on the one hand specify in what respect a pair of objects is similar, but on the other hand is simultaneously capable of indicating in what respect they differ. The oddity-from-sample paradigm as used by us tends to force pigeons to disregard variations along the invariance dimensions when choosing among alternative stimuli along the discrimination dimension. Many other discrimination paradigms do not incorporate such biasing. But even in our experiments the pigeons may not have been insensitive to the variations on the invariance dimensions. The time they took to decide about the oddity of shapes was consistently lengthened in all experiments when the relevant stimuli differed with regard to the invariance features. Unfortunately, however, we cannot completely exclude the possibility that this effect was due to stimulus novelty since the corresponding tests always involved shapes that were novel to the subjects.

The present results have one further implication. In every experiment the critical test stimuli used were novel to the pigeons. Nonetheless, without any additional learning (as the test sets were presented under extinction conditions), the birds chose correctly among them according to the oddity-from-sample principle they had previously learned to use. There can thus be little doubt that pigeons can apply a relational, conceptual rule in the matching/oddity paradigm (Lombardi, Fachinelli and Delius, 1984; Edwards, Miller and Zentall, 1985; Pisacreta, Lefave, Lesneski and Potter, 1985; Lombardi, Delius and Hollard, 1986; Wright, Cook, Rivera and Delius, 1988) rather than only stimulus or configuration specific rules as several other authors maintain (Carter and Werner, 1978; Mackintosh, 1983; D'Amato, Salmon, Loukas and Tomie, 1985). The present results considerably discredit the suggestion that our pigeons somehow solved the oddity task when faced with novel shapes on the basis of simple chance similarities between the stimuli constituting the training sets and those constituting the testing sets. The profusion of training and testing stimuli we used makes this a highly improbable proposition. An alternative suggestion is that all the pigeons learned and applied was a rule of choosing the odd luminous flux in the experiment by Lombardi et al. (1986). This suggestion can now easily be

rejected. All 3 present experiments involved luminous flux modifications of the comparison shapes during the test components that make that rule inapplicable. Nonetheless the pigeons continued to transfer well to stimulus constellations constructed from shapes novel to them.

In a way we have the reverse problem on our hands and that is to explain why the oddity transfer performance in two of the present experiments was so good. In the original study of Lombardi et al. (1984) the pigeons' transfer performance on unreinforced novel test sets had not exceeded 83.2% correct choices. In this study the analogous transfer test with the best results yielded as many as 95.1% correct responses, even though the test in question was complicated by a distracting color cue. The obvious explanation for this improvement in our opinion is the considerable additional experience that the animals had had with the oddity-from-sample task. Since the original tests they had dealt with several dozen additional stimuli and had completed many tests with novel patterns (Lombardi and Delius, 1989; Lombardi, 1989). Lombardi et al. (1984) and Wright et al. (1988) had already argued that a large number of training exemplars and a thorough novelty immunization were likely to be important factors for the dominance of concept-governed behavior in pigeons. We cannot exclude, and in fact suspect that other, more subtle factors may also be important. A candidate factor that interests us at present is the differing degrees of spontaneous attention that stimuli of various qualities appear to command from pigeons.

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BEHAVIORAL ADJUSTMENTS OF CUCKOO NESTLINGS (*CUCULUS CANORUS*) TO FOSTER PARENTS

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ABSTRACT: The behavior and adjustments of a cuckoo nestling developing in a redstart nest were studied. High acoustic sensitivity was found in the range of non-species-typical components of the sonic feeding complex of the host species. The general tendency of avian hearing development, accelerated formation of low-frequency range, also plays an important role in the biology of the parasite species. A constantly increased level of feeding motivation along with the high acoustic sensitivity are basic for the 100% responsiveness to arrivals of adults with food. Vocalization matching, that is, a coincidence of the frequency band limits and of the intensity of vocalization of a cuckoo chick and redstart brood ensures the equal frequency of feedings. The coincidence of sequence and timing of the periods of nest life of cuckoo and redstart young that were determined with respect to the change of the modality stimulating feeding behavior increases the feeding competition abilities of a cuckoo nestling in the case of forced coexistence with the young of the host species.

The most prominent and well-known characteristic of the behavior of the nestlings of the nest parasite, the common cuckoo (*Cuculus canorus*), is the fact that immediately after hatching they start throwing the eggs and nestlings of their foster parents out of the nest. This behavior has been observed in all sub-species of the common cuckoo that parasitize the nests of different passerine species, both open- and hole-nesters. The adaptive meaning of this behavioral pattern, the elimination of competitors for food, seems so obvious that time has failed to affect this view postulated decades ago (Promptov, 1941; Malchevsky, 1954, 1987; Gould & Marler, 1987). This is probably because the behavior of cuckoo nestlings has remained the subject of naturalistic description (Malchevsky, 1987) rather than the focus of an experimental analysis. The majority, if not all, researchers concentrated their attention on the egg-throwing behavior itself. According to the logic of the traditional

approach, a cuckoo nestling would starve if it did not successfully dispose of its possible future "nest-mates." However, in two cases foster parents were seen successfully feeding their own young and a cuckoo chick in deep tree-holes where the latter could not effectively dispose of the foster species' eggs (Malchevsky, 1954; Shkatulova, 1970). These are the only reports we know of the adjustments of cuckoo nestlings to the nest-life of their foster parents other than the behavioral pattern of eggs and/or nestling removal.

The present study was designed to analyze the sensory basis of the main behavioral patterns of the postembryonic ontogeny of common cuckoo nestlings reared by redstarts (*Phoenicurus phoenicurus*). The focus of the study was on the adjustive characteristics of the behavior of the young throughout the period in the nest, 20 days for the cuckoo and 14–15 days for the redstarts. Our analysis of the organization of feeding behavior of the young was aimed at the evaluation of the probability of a feeding reaction by the young to an arrival of an adult with food and the probability of reinforcement of these reactions (begging success) for each nestling during each day of nest life. In the studies of the families in which cuckoo nestlings were reared, special attention was paid to the stimuli eliciting feeding and defense reactions in cuckoo and redstart chicks and to the organization of their behavior.

METHODS AND PROCEDURES

All field and laboratory studies were carried out in the Oka-Terrace State Reserve (120 km south of Moscow).

Field Studies

Artificial wooden nest-boxes (13 x 13 x 30 cm) were set up 1.5–2 m above the ground on tree trunks in the mixed forest. From May through July these nest-boxes were used for breeding by various hole-nesters: pied flycatchers (*Muscicapa hypoleuca*), different tits (*Parus spp.*) and occasionally by redstarts. Birds constructed their nests in the center on the bottom of the nest-boxes, approximately 15 cm below the entrance hole.

To study the nest behavior we constructed a wooden light-protected experimental chamber (1.5 x 1.5 x 1.5 m) that housed researcher and all necessary equipment near the nest to be studied. The experimental nest-box that was fixed in the wall of the chamber differed from an ordinary one only in that its back wall could be easily removed to observe the nest. During the observation period adult redstarts (both male and female) were foraging on their own. The observer and the equipment in the dark experimental chamber did not in any way influence the normal nest life of the birds under study.

The only criterion for a choice of a given redstart family from the local population was the presence of a cuckoo egg in the clutch. One such family was found and studied each season. Observations were made during two breeding seasons successively throughout the period of cuckoo nest life (20 days). Nest behavior was observed during the light hours (10 to 12 h) of continuous observation starting every day at 0600-0700 h.

Each nest was divided into 13 zones: a central zone and 12 sectors, numbered clockwise. In all families studied the following data were recorded daily in the protocol: the time of hatching of each nestling; stimuli eliciting feeding and defense reactions of the young; sectors occupied by the parents on the nest edge during feeding the young; zones of the nest where begging of each of individually marked chick took place; number and position of the nestling that got food during each feeding act; and nestling body weight.

Sounds emitted by the young and their parents were tape-recorded. The microphone of the tape-recorder and the 1.5 cm microphone of a Bruel & Kjaer (Type 2203), SPL-meter to measure intensity of vocalization were placed 15 cm above the center of the nest. Sounds were analyzed on a Kay Electric 7029A sonograph with narrow-band filter in the frequency band of 0-16 kHz.

Each season one family with only five redstart chicks and a family with one cuckoo chick to which one redstart chick was later added were studied. These were obtained in the following way. A few days before hatching a redstart nest with six eggs, including one laid by a cuckoo, was removed from the nest-box on a tree into the experimental chamber. After the cuckoo young had hatched, the redstart eggs were moved to the redstart nest in the other experimental chamber. The redstart eggs of the second family were distributed among other redstart broods. In both cases redstart young hatched 1-1.5 days after the cuckoo; thus, cuckoo nestlings were 1-1.5 days older than their redstart "siblings" in the study. When the cuckoo was six days old and had stopped attempting to throw redstart nestlings out of the nest, a 4.5 day-old redstart chick was returned to its native nest to join the cuckoo chick; thus the original age difference was maintained.

Laboratory Studies

Laboratory studies were performed in the laboratory building containing all necessary equipment. Nestlings to be observed were brought from their nests, which usually took 5 to 15 min. After the procedures that lasted 20-45 min, chicks were quickly delivered back to their nests.

Auditory Sensitivity. The range of auditory sensitivity of cuckoo and redstart nestlings was measured daily between days 1 and 6. Nestlings were placed one by one in the nest 15 cm from the loudspeaker.

Gated signals from the sound generator were used. After testing each nestling, the microphone of the Bruel & Kjaer SPL-meter was placed in the nest in the position of a nestling's head to measure the threshold intensity.

Monotonic signals 100 ms duration, 5 ms rise/fall, in the frequency range 0.1–6.0 kHz, in steps of 100 Hz, were presented in a quasirandom order. The criterion of auditory sensitivity was feeding reactions by nestlings at the highest level of feeding motivation to 90% of the presented stimuli.

Other Stimuli Eliciting the Feeding Reaction. Nestlings were presented with soundless light flashes of varying intensity and duration generated by an FS-2 photostimulator. The vibration sensitivity was tested by means of shaking the nest with a chick in it, with special precautions taken against rustling of the nest material that was an effective stimulus by itself for begging. Sensitivity of the nestlings to an air flow from a bicycle pump was tested.

RESULTS

Development of Behavior in Redstart Young. The dominating behavior pattern in 1–5 day old nestlings was feeding. Under natural conditions begging was elicited by a cluster of stimuli which may be called the sonic feeding complex: 1) the sound made by the feet of an adult bird landing on the nestbox; 2) the rustle of the material in the nest caused by the bird's landing on the nest edge and 3) the species-typical food call, emitted by a bird. The characteristics of redstart parental signals are presented in Table 1 and Figure 1.

Beginning with the first day of life, the feeding reaction of the nestlings was accompanied by their vocalizations. By day 4 it reached a level high enough for measurement and recording by the equipment used. Sonographic analysis revealed (Fig. 2) that these sounds were in the wide frequency band between 4.0 and 8.0 kHz, the borders shifting towards the low-frequency part of the spectrum as the chicks grew. Changes in the integrated level of the vocalization intensity of the redstart brood consisting of 5 chicks are illustrated in Figure 3. In response to the sonic feeding complex nestlings changed their posture: the body was oriented vertically, the neck was stretched upward, the beak was opened wide. The very first begging response included a vocalization component of low intensity. The parents stayed in the nest-box when the young did not need warming after one of the chicks had received a portion of food as long as the chicks vocalized and moved in the nest (4.6 ± 0.3). The adult bird left the nest after picking up the fecal capsule of the young or after there was no chick movement. Movements and vocalizations ceased simultaneously.

When the modality and the parameters of stimuli effective for begging in 1-5 day old young were studied in the laboratory it was found out that begging could be elicited *only* by the *acoustic signals*. Begging in chicks with the highest level of feeding motivation (Khayutin, 1985) could be provoked in the laboratory not only by playing a tape recording of the sonic feeding complex but also by a rich assortment of sounds, e.g., human whistles and speech. No other stimuli, such as tactile (e.g., air flow), vibrational or visual could elicit begging in the young at that stage. Khayutin (1985) also found this to be true of other hole-nesters, such as *Erithacus rubecula*, *Ficedula hypoleuca*, *Parus major*, and *Parus atricapillus*.

When feeding sounds were imitated in the laboratory by a wide range of signal tones, auditory sensitivity was found in the range of 0.1-5.1 kHz. The lowest thresholds were in the 0.1-0.2 and 1.5-2.5 kHz

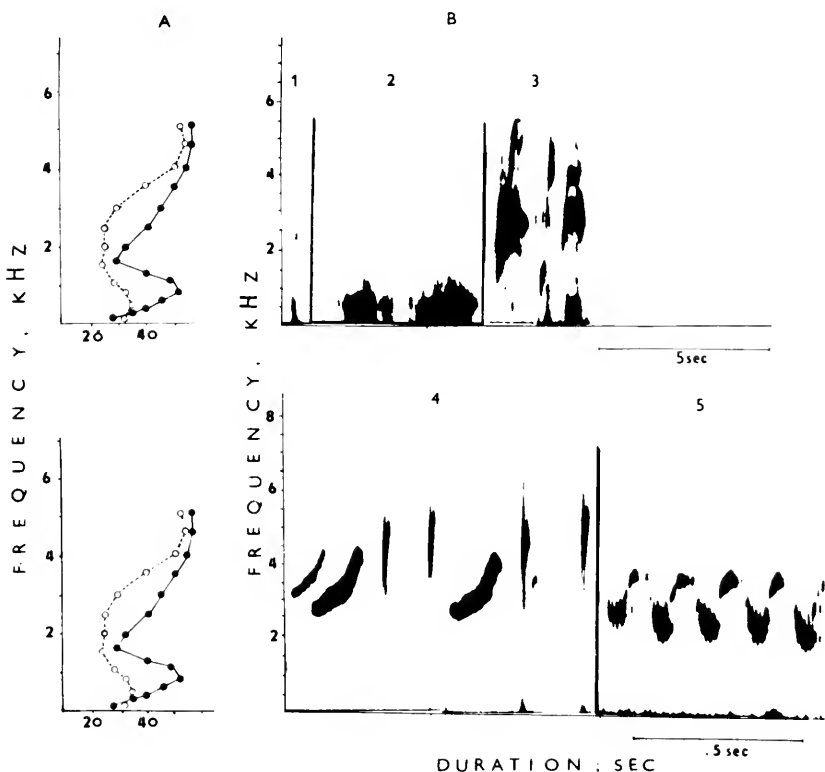


FIGURE 1. A. Auditory thresholds of 5-day nestlings: 1. redstart; 2. cuckoo; dB above the background noise level. B. Sonograms of sounds produced by parental redstart behavior meaningful for young behavior. Sonic feeding complex; 1, parent feet tapping; 2, rustling of nest; 3, variations of the food call. 4. Alarm call. 5. Species song.

TABLE 1
Characteristics of Parental Acoustic Signals of
Redstarts Recorded in Natural Nests

<i>Signals</i>	<i>Main energy maxima (kHz)</i>	<i>Duration (ms)</i>
Sound of feet tapping on a nest-box	0.2-0.75 1.5-2.50 3.5-4.00	50-75
Rustle of nest material from landings on a nest	0.2-1.25	200-500
Food call	0.2-0.80 2.0-3.50 3.5-5.50	50-100
Alarm call	2.5-3.50	25-150

ranges. A comparison of the hearing range of the young with the spectrum of the sonic feeding complex (Figure 1B, 1-3) revealed that the first of these sensitivity peaks corresponded to the maximum energy of the first two components of the complex, while the second peak corresponded to the high-energy part of the food call (Figure 1A, 1). The first two components of the sonic feeding complex have characteristics that are not restricted to redstarts, while the third, the food call, is characteristic only of the redstart species.

Beginning with day 5, nestlings started to show a passive-defense reaction, that is, a cessation of vocalization and freezing, in response to the alarm call. On day 5-6, the nestlings' eyes opened and the modality of the stimulus for feeding behavior changed significantly. Beginning with days 5-6 and until day 8, when the visual system responded only to diffuse light, the diffuse luminosity change caused by the arrival of the adult bird with food that closed the entrance hole with its body became the dominant component of the complex of feeding stimuli in the natural nest box. As a result, the frequency of occurrence of the food call was reduced greatly; it was observed in 10% of the feedings only. In spite of the significant increase of the variety of feeding stimuli, i.e., the appearance of a new stimulus modality, no changes in the pattern of feeding took place until day 8-9.

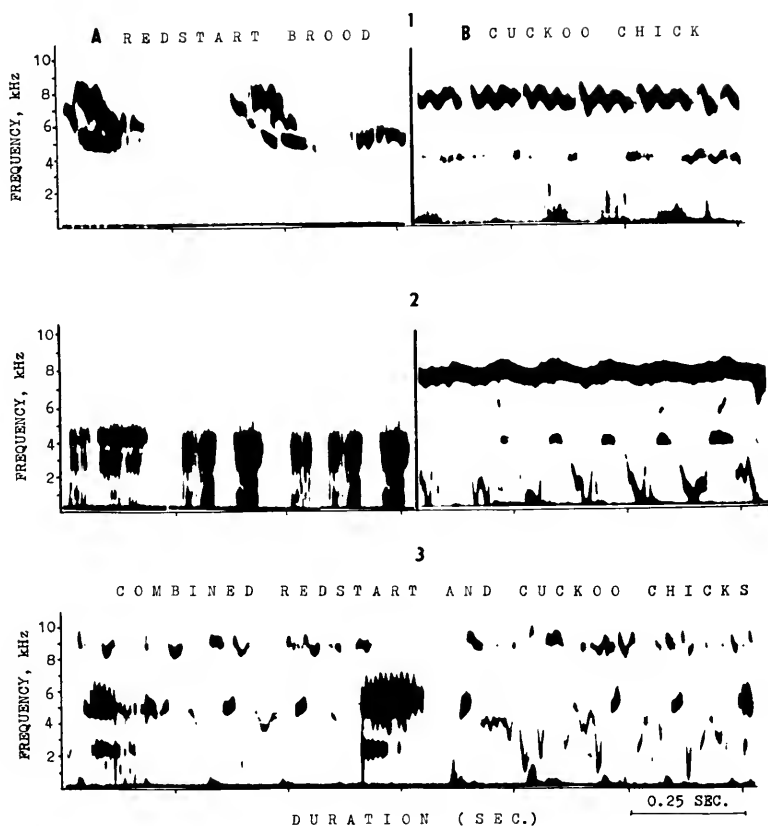


FIGURE 2. Vocalization component of begging behavior of redstart brood (A) and of cuckoo chick (B). A, 5-day old chicks; 12-day old chicks; 3, vocalization accompanying begging of redstart chick sharing the nest on 8-day old and 9.5-day old cuckoo chick.

On day 8 the feeding reaction was transformed from passive begging to active food-acquisition. The young turned their heads to the head of the parent and tried to snatch the food from its beak. Until day 11, this behavior followed a change in diffuse luminosity and was guided by the moving silhouette of the adult. Food acquisition was elicited and guided by the moving bird silhouette after this and until fledging.

In general, the distribution of food in the brood of redstart young was like that described for some other species (Khayutin & Dmitrieva, 1976; Best, 1977; Khayutin, 1985). Even distribution of food among the young was due to their relatively regular circular movement in the nest. Each nestling periodically occupied the zone with the highest probability of begging success as it moved around the nest. These zones were connected with the places taken by the parents for feeding the young, the places being fixed in any given nest (Khayutin & Dmitrieva, 1981).

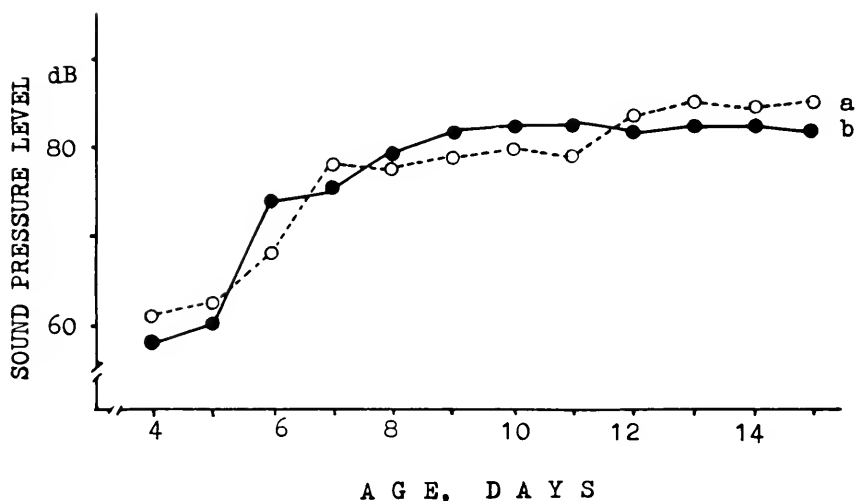


FIGURE 3. Intensity of vocalization of redstart brood of five nestlings (a) and cuckoo chicks (b).

Most arrivals of adults provoked begging in at least four chicks or in all young, i.e., the probability of begging for each nestling in response to each arrival of a parent was 70-90% (Fig. 4A, 2) but only one chick got food. After a chick in the optimal zone got food, it left the area and, by the time of the next arrival of a parent, this zone was usually occupied by another young. Thus in a brood of five, each nestling got 20% of all food brought by the parents, each of the young having only one of four or five beggings reinforced. The fact that the probability of reinforcement of each nestling was slightly higher than 20% (Fig. 4B, 1) might be due to two reasons: a) the probability of begging for each young was somewhat below 100%; b) sometimes, though rarely, that is, in 2-3% of all feedings, birds did feed more than one nestling at a time.

Body weights of nestlings yielded the S-shaped curves typical for altricial birds (Poznanin, 1979; Khayutin & Dmitrieva, 1981). By day 11, the young reached the maximal mass of 15 g that varied only slightly during the last days in the nest (Fig. 5, 1).

Behavioral Organization of the Cuckoo Nestling. Immediately after hatching the cuckoo young was observed begging and throwing eggs and/or nestlings out of the nest. The latter pattern has been described in numerous studies (Promptov, 1941; Numerov, 1978).

The analysis of the feeding behavior in the cuckoo nestling revealed that the redstart sonic feeding complex elicited its begging. The motor organization of begging in the cuckoo young differed from that of the redstart: the reaction was tonic and included no apparent movements of body and limbs. The neck was bent backwards and the position of the

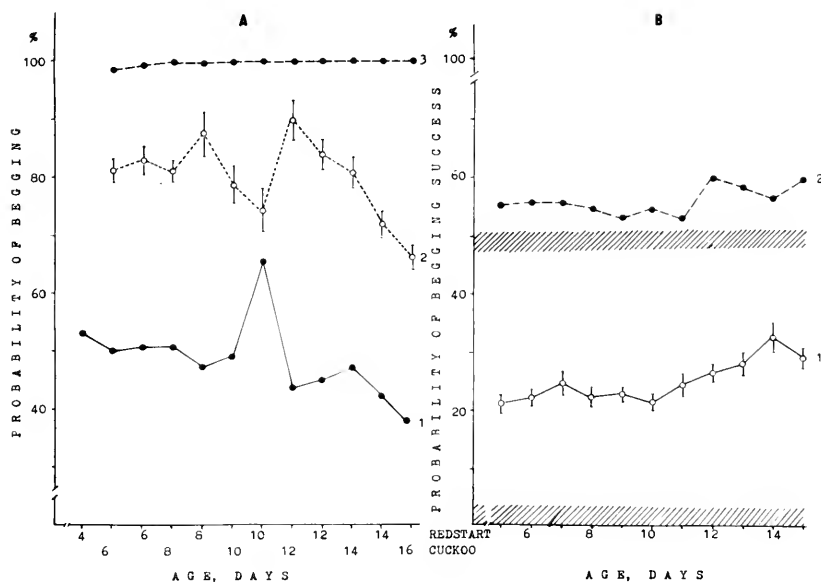


FIGURE 4. A. Probability of the feeding reaction (begging) in 1) redstart chicks ($n=2$); 2) 5 redstart chicks in a normal brood sharing one nest ($n=10$); and 3) cuckoo chicks ($n=2$). B. Probability of begging success for a redstart nestling developing 1) with 4 siblings ($n=10$); and 2) with a cuckoo chick ($n=2$). Area between hatch lines = expected probability of begging success for a redstart developing in a nest with a cuckoo chick.

head was fixed with the beak wide open. This posture was maintained until the adult left the nest-box. Begging included a vocalization component that reached a measureable level by day 4-5 (Figure 2B, 1). The vocalization of a 4-5 day-old was frequency modulated, narrow-banded with two marked energy maxima at 4.0-4.5 and 7.0-9.0 kHz and with a low-frequency component of 0.1-2.5 kHz. The latter is a sonographic representation of a click. As the nestlings grew older, the low-frequency component became more marked and its structure more complicated (Figure 3, B).

The auditory sensitivity of 1-6 day-old nestlings was in the range of 0.2-5.1 kHz; sensitivity peaks corresponded to 0.2-0.4 and 1.6-2.0 kHz. Comparison of the hearing range of cuckoo young with the spectrum of the sonic feeding complex of the foster parents revealed that the low-frequency sensitivity peak corresponded to the energy maxima of the first two components of the complex while the second peak corresponded to the high-energy part of the species-typical redstart food call (Fig. 1A, 2).

We also tried to find some other stimuli eliciting feeding behavior in cuckoo chicks: light flashes of varying intensity and duration, air flow,

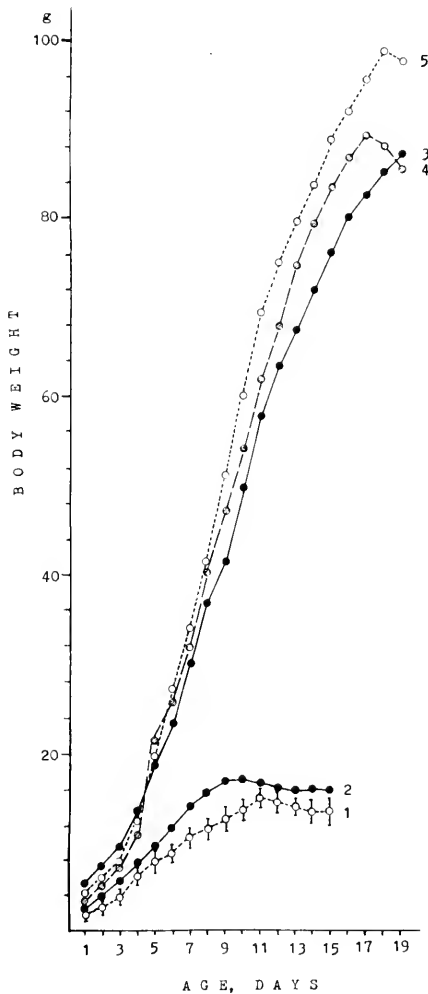


FIGURE 5. Body weights of nestlings. Redstart chick: 1. in a normal brood ($n=10$); 2. sharing a nest with a cuckoo ($n=2$). Cuckoo chick developing alone 3) after Promptov (1941) ($n=12$) and 4) after Numerev (1978) ($n=8$); and 5) developing with one redstart chick ($n=2$).

shaking of the nest. Only the latter, of all stimuli used, elicited begging in the cuckoo chick.

Cuckoos opened their eyes on day 6. This was accompanied by the emergence of a feeding reaction in response to a diffuse luminosity change. However, the sounds produced by the arriving adult bird remained very effective stimuli for begging until the end of the nest period. From day 6 the cuckoo chicks stopped vocalizing and froze to the alarm calls of foster species and some other birds (passive-defense

reaction). But if a parent arrived with food, or if the feeding stimuli were reproduced artificially while an alarm call sounded outside the nest-box, the cuckoo chick immediately started to beg, either in complete silence or with barely audible vocalization. In response to repeated stimulation this reduced begging was quickly substituted by a normal one. In redstart chicks such suppression of defense reactions was observed very early.

On day 11 the moving parent started to provoke a very active food-acquisition response. No changes in the behavior of the young were observed from day 11 to the end of the nest period (day 20). Begging was elicited by the sounds produced by the arriving bird and by its moving silhouette.

Development of Cuckoo and Redstart Chicks in a Shared Nest. In an attempt to understand what made the foster parents feed cuckoo chicks that differed greatly from their own young in body size, feather coloring, as well as in size and color of the oral cavity, we analyzed the behavior of adult birds and cuckoo and redstart nestlings sharing the same nest. When the cuckoo was 6 days old, a 4.5-day old redstart was placed in the nest. By that time both had their eyes open and thus begging was adequately stimulated by the luminosity change as well as by sonic stimuli. Although the hearing range and sensitivity peaks of the cuckoo chicks matched those of the redstart young, its low-frequency thresholds (corresponding to energy maxima of the nonspecific components of the complex) were 1.5–2 times lower than those of redstarts. However, in the high-frequency range corresponding to the spectrum of the redstart food call, the cuckoo's absolute thresholds were a few times higher than those of a redstart chick of the same age. Cuckoo chicks responded by normal begging to the same set of sounds that caused a feeding response in redstart young.

Feeding was organized as follows. All arrivals of an adult elicited begging in the cuckoo chick, but only 45% of the arrivals elicited begging in the redstart (Fig. 4A, 1, 3). Thus, in 45% of the cases, the nestlings responded in a chorus. Here it is worth noting that in normal redstart broods of five, each young reacted to 70–90% of the arrivals while the probability of begging success could not significantly exceed 20%. From this the following somewhat arbitrary conclusion may be inferred: if redstart parents feed each of the two chicks with equal willingness, as in the case with a normal brood of five redstart chicks, the probability of reinforcement of a feeding reaction in each of two different young must be about 50% (Fig. 4B, upper hatched line). Reports from other studies, however, challenge such an oversimplification. Adult birds are known to put food selectively in the most widely opened beaks when feeding differently-aged nestlings (Lohrl, 1968; Illies, 1975). Considering the great differences between the cuckoo and redstart nestlings in the body

size and the size of the opened beaks, it may be supposed that the redstart's begging should practically never be reinforced (Fig. 4B, lower hatch lines). Thus the probability of begging success for a redstart sharing the nest with a cuckoo must be confined within the limits of 0-50%.

The analysis of the distribution of food between two different chicks in each of the nests during the two seasons throughout their joint stay in the same nest revealed, however, that the probability of reinforcement of the redstart's feeding response reached 60%, that is, it exceeded the expected level (Fig. 4B, 2). How can this high probability of the redstart's begging success be explained in view of the fact that the redstart's feeding reactions themselves occurred much less frequently than did those of the cuckoo as well as less frequently than those of the other redstart chicks (Fig. 4A, 1, 2 and 3).

As noted above and elsewhere (Khayutin & Dmitrieva, 1981; Khayutin, 1985) the existence and location of the zones with the highest probability of begging success was determined in each nest by the places taken by the parents on the edge of the nest when feeding the young and by the adult's physical ability to bend its neck and put food into an open beak of one of the young. When a cuckoo chick and a redstart chick were begging, in spite of the fact that the central part of the nest was occupied by the cuckoo, and the redstart chick was pressed into a distant sector of the nest with the most unfavorable position for feeding, the redstart chick was fed more often. Moreover, when feeding its own young, an adult bird was often carrying food right in front of the open beak of cuckoo young

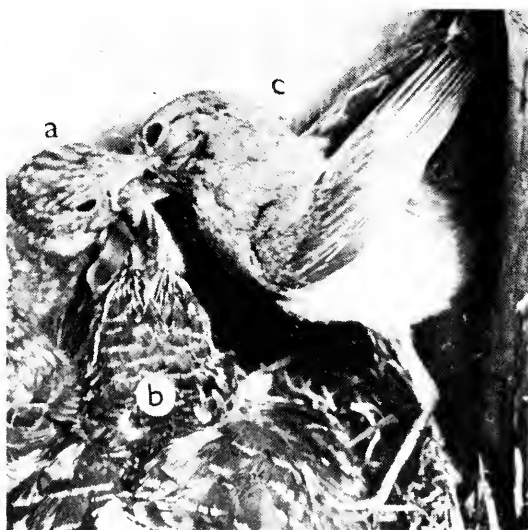


FIGURE 6. Redstart (C) selectively feeding its own nestling (A) developing in the nest with a cuckoo chick (B).

provoking its violent attacks (Fig. 6). On many occasions (55%) the sounds produced by an arriving parent that always elicited a feeding response in the cuckoo, appeared ineffective for the redstart chick because of its constantly decreased level of feeding motivation. In those cases, the parent emitted the food call that was never used when feeding the young with open eyes in normal broods. This call provoked a very slow feeding response in the redstart chick that was immediately reinforced (Fig. 6). Sometimes adults even tried to force food into the beak of their own chick.

DISCUSSION

Our observations indicated the existence of a very finely-tuned parental behavior manifested in the selective feeding of the young of its own species by the parent. As the foster parent's chicks have the "first turn" during feeding, the specific behavior pattern in which cuckoo young throw out the eggs and/or nestlings of the parasitized species may be considered an elimination of the competitors for food that are preferred by the cuckoo's foster parents, rather than resulting from hypothetical limitations of food resources or from the limited physical capabilities of the foster parents.

The unique role of these two factors, the availability of resources and parental prowess, are widely accepted and cited in the ornithologic and behavioral literature. For example, Manteifel says (1980, p. 16), "This whole complex of behavior of a newborn cuckoo is unequivocally inborn and was developed in the evolution of the parasitic species as a necessary adaptation, because a pair of small passerine foster parents is barely able to feed one very voracious cuckoo chick which grows extremely quickly. They cannot feed and raise their own brood in addition to the adopted child." This viewpoint is contradicted by the data of Malchevsky (1954) and Shkatulova (1970) who observed foster parents successfully feeding cuckoo chicks as well as their own young. Our own data (Figure 5) demonstrate that the body weights of cuckoo young raised with redstarts are no less than the body weights of cuckoos raised alone and that the body weights of redstarts raised with cuckoos are also less than those raised with other redstarts.

Marked parental preference for their own young results in an apparent ignoring of the cuckoo chick during its life in the same nest. From this observation it may be supposed that foster parents probably do to some extent ignore a cuckoo chick even when the foundling is alone in the nest. Consequently, cuckoo nestlings must possess a set of adaptations that can counteract this tendency. On the basis of our observations the following traits may be suggested as the possible candidates for such adaptations:

1. High sensitivity of sensory mechanisms to the feeding behavior stimuli addressed to the young of the host species.
2. A constantly increased level of feeding motivation that along with the sensitive sensory mechanisms ensures the 10-80% responsiveness of the cuckoos to the arrivals of the adult birds.
3. The match between the upper and lower limits of the frequency bands and amplitude of vocalization of one cuckoo chick and of a brood of five redstart chicks, which is most marked at the early age. Khayutin & Dmitrieva (1981) have shown that the vocalizations of an entire brood of chicks acted as an index of the integral level of the feeding motivation that regulated the frequency of feeding. The equivalent intensities of the vocalization of a cuckoo chick and five redstart nestlings may determine the similar frequency of the feeding episodes in both cases.
4. The bright coloring and larger size of the cuckoo oral cavity may partly counteract the tendency of the redstart parents to feed their own young selectively. Thus the cuckoo can take advantage of the basic "conservatism of parental behavior" that leads to the selective feeding of bigger nestlings.
5. The match of the succession and timing of the stages of nestling development that are related to the changes of the modalities of the stimuli that elicit feeding behavior in cuckoo and redstart young. This match may be considered to be a *super-adaptation* that is realized in case of the failure of the cuckoo's first adaptive behavior pattern, i.e., throwing out eggs and/or nestlings. This superadaptation increases the cuckoo's feeding competitiveness significantly when it has to share the nest with the young of the foster parents, but is not necessary in the case of solitary development.

SUMMARY

The survival of the parasite species, *Cuculus canorus*, is based not only on the efficacy of the behavioral adaptations of adult cuckoos (e.g., the selection of adequate nests and the timing of egg-laying) but also on the adaptational mechanisms that their young possess. Some of these mechanisms have been revealed in this study. The most widely known pattern is throwing eggs and/or nestlings out of the nest. Other behavioral and physiological mechanisms may also play an important role in the survival of a cuckoo in the nest of foster parents. The first concerns the timing of maturation and the range of thresholds of cuckoo auditory

sensitivity. Our comparison of the cuckoo chick's hearing range and the spectrum of adult redstart feeding sounds has demonstrated that the peaks of auditory sensitivity matched the energy maxima of those components of the sonic feeding complex that were not species-typical, the thresholds in that range being two times lower than those of redstart young. The well-known general tendency of the hearing development in the low-frequency range (Golubeva, 1978; Konishi, 1973; Saunders, Cole & Gates, 1973; Ryden, 1980) and the relation of hearing to early behavior patterns including feeding (Milyagin, 1957; Gottlieb, 1971; Khayutin & Dmitrieva, 1981), increase the efficacy of the organization of feeding behavior in parasitic nestlings ensuring their adequate reaction to the nonspecific as well as to species-typical components of the sonic feeding complex of the foster parents.

Along with the characteristics of hearing, we studied other sensory factors of cuckoo chick feeding behavior and found that they were sensitive to vibration (soundless shaking) of the nest. No other nestling of any hole-nester species studied displayed begging in response to shaking in spite of the highest possible level of feeding motivation. On the other hand, this factor was described as an element of a signal complex of feeding response in rook nestlings by Milyagin (1946) and in blackbird young by Manteifel (1980). These findings suggest that the sensitivity to vibration and its relation to feeding behavior is a common characteristic of the nestlings of big open-nesters with nests on branches, for only then would the arrival of parents with food result in nest shaking.

Thus, cuckoos parasitizing redstart nests possess in their early ontogeny a capability to display a feeding behavior pattern in response to a wider complex of stimuli of different modalities than is necessary for survival; an adequate feeding response not only to sounds but also to vibration might theoretically help its nestlings survive not only in the nests of hole-nesters but even in the nests of big open-nesters that make nests in the trees.

In spite of the fact that after the cuckoo's eye had opened, and the modality stimulating feeding behavior changed, so that chicks started to respond to luminosity changes, sounds still remained highly effective and were related to begging until fledging. Such a high degree of efficacy of acoustic signals for the realization of feeding behavior until the end of nest life is also atypical for redstarts and any of the hole-nesting species studied by us (Khayutin & Dmitrieva, 1981; Khayutin, 1985).

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USE OF VISUAL AND TACTUAL CUES IN LEARNING OF SIMULTANEOUS SHAPE DISCRIMINATIONS BY ALBINO AND PIGMENTED RATS (*RATTUS NORVEGICUS*)

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ABSTRACT: Albino Wistar, pigmented DA and crossbred (F_1) rats were compared in learning of 4 versions of a simultaneous circle-triangle discrimination. On tasks with 3 dimensional shapes, either with both visual and tactual cues available, or without the tactual cues, albino rats performed as well as the pigmented rats. On tasks with reduction of visual cues, (one task with 2 dimensional cues, the other with tactual cues, and reduced 3 dimensional visual cues), the albino group's performance was significantly inferior to that of the pigmented rats. The two types of pigmented rats did not differ in learning on any task.

In the present study we have examined the differing propensities of albino and pigmented rats to use strong or weak visual cues and tactual cues in the learning of four versions of a simultaneous shape discrimination task.

Albino rats have been used extensively in studies involving visual discrimination (e.g. Bennett & Anton, 1972; Bennett & Ellis, 1968; Gibson & Walk, 1956; Kerpelman, 1965; Oswalt, 1972) in spite of defects in the albino visual system. Albino rats have poorer visual acuity compared to pigmented rats as measured by their thresholds for detection of striations (Lashley, 1930; Montero, 1973). The pigmented (gray) rat's optic nerve has larger axons with thicker myelin (Fukuda, Sugimoto & Shirokawa, 1982; Sugimoto, Fukuda & Wakakuwa, 1984). The albino rat does not show optokinetic nystagmus or vestibular nucleus activity to optokinetic stimuli as is seen in the pigmented (DA) rat (Precht & Cazin, 1979). In the albino there are aberrant retinal projections to the lateral geniculate nucleus (Guillery, 1974), and more of the visual field is represented by uncrossed optic fibres with deficient projections in the visual cortex (Lund, Lund & Wise, 1975). Such visual system differences appear to be

correlated with lack of pigment in the pigment epithelium of the retina (Lavail, Nixon & Sidman, 1978; Wise & Lund, 1976).

In view of these differences it would not be surprising to find that pigmented rats perform better than albinos on visual discrimination. This is, however, not always the case. In earlier studies we have found that, after undergoing a pre-training exposure condition, albino rats were inferior to pigmented rats in the rate of learning of a three dimensional shape (circle versus triangle) discrimination, with both visual and tactual cues available. However, for control animals given no prior exposure to the cues, albino and pigmented rats did not differ significantly in the learning of the discrimination task (Bell & Livesey, 1981).

This finding that, in spite of an inferior visual system, the albinos performed at a level comparable with that of the pigmented rats in the control condition became our focus of interest in the current experiment.

In other studies involving pre-exposure to discrimination cues, investigators have found that albino rats needed three dimensional cues (tactual and visual) to solve shape discriminations. Albinos were not able to learn a two dimensional shape discrimination unless given lengthy prior and simultaneous exposure to three dimensional (3D) shapes (Gibson & Walk, 1956). If such exposure was to two dimensional (2D) shapes, rats did not learn the discrimination (Walk, Gibson, Pick & Tighe, 1959). Bennett and Ellis (1968) demonstrated that exposure in which albinos were able to manipulate the 3D forms, led to significantly better learning of the 2D task, compared with visual only exposure to the 3D forms. They argued that this was probably the result of tactual/kines-thetic feedback. In exposure experiments with pigmented rats, however, visual-only 3D cues were found to be effective in enhancing discrimination learning, with opportunity to manipulate the shapes providing no extra gain (Bennett, Rickert & McAllister, 1970).

In view of the above findings it seemed likely that, in our control condition (Bell & Livesey, 1981), the albinos made use of both the visual and tactual cues, possibly relying more strongly on the tactual information, while the pigmented animals made more use of the visual information. In the present experiment we set out to resolve whether albino rats do use a different strategy than do pigmented rats in solving this discrimination task, and in comparison, how they performed on the shape task without tactual cues.

For this purpose we utilized four versions of the circle-triangle discrimination which differed in availability of visual and tactual cues. A simultaneous discrimination paradigm was employed in a within experiment comparison of albino and pigmented rats. The tasks employed were (i) the previously used three dimensional, visual/tactual discrimination (VT), (ii) the three dimensional discrimination without access to the tactual cues (3DV), (iii) the 3D task with the tactual cues but with

markedly reduced visual cues (TRV), (iv) a task with two dimensional visual cues only (2DV).

In our previous experiments, the albino rats used were from a Wistar strain and the pigmented rats a DA strain. These were not inbred groups and, in addition to differing in terms of the albino gene, the two stocks were known to differ in coat colour genes; the DA rats being homozygous for the agouti allele (AA), while the Wistars were homozygous for non-agouti (aa); and they also differed at the white spotting or hooding locus (HH versus hh) and the brown locus (BB versus bb) (Robinson, 1979). These coat differences were established in the two stocks we were using by a crossbreeding programme, examining F_2 and backcross progeny. Strain differences other than those associated with the albinos' visual anomalies might conceivably be important in a learning context. For example differences in reactivity could have differential effects on discrimination learning (e.g. Cowan, 1977; Harrington, 1971). Because of this and to gain further information on differences between different types of rat, we included a sample of crossbred (F_1) rats, the offspring from Wistar-DA matings. The learning patterns of these heterozygotes could thus be compared with those of the parent strains. While the F_1 rats were pigmented and therefore had the same pigmentation of the eye as the DAs, they did not have the particular phenotype of either strain. It is reported too, that animals heterozygous for albinism do share some of the visual neural deficits of albinos though not to the same extent, e.g., hooded rats show some reduction in optic nerve axons and myelin (Fukuda, et al. 1982).

Thus, in this experiment, separate groups of Albino Wistar (W), Pigmented DA (DA), and F_1 rats were given the four versions of the circle-triangle discrimination. In view of our earlier finding (Bell and Livesey, 1981) it was anticipated that albino rats would perform as well as pigmented animals on the VT task. Evidence from other studies indicated that the DA rats would be superior to W rats learning the 2DV task. If the albinos rely more on tactual than on visual cues to solve the VT task then we would expect them to perform at least as well as the DA animals on the TRV task but not on the 3DV task. We expected that the DA rats would do equally as well on the 3DV as on the VT task. If the differences in learning between the DA and W rats were due to differences in visual capability and not significantly affected by other strain differences, then the F_1 rats would not differ significantly from DA rats in learning of these tasks.

METHOD

The design of the experiment was a three by four factorial: with three types of rat (W, DA & F_1) and four tasks: (VT, 3DV, 2DV, and TRV).

Animals

(a). Thirty-two albino rats from Wistar stock (W1MWA) of the Animal Resources Centre (ARC), Murdoch, Western Australia. A closed breeding colony had been maintained for 20 years at the University of Western Australia prior to transfer to the ARC in 1981. It is believed that the stock originally came from Adelaide, South Australia. (b). Thirty-two rats from DA stock of the Psychology Department, University of Western Australia. This colony was established in 1973, with stock from the Walter and Eliza Hall Institute of Medical Research, Victoria, Australia. (c). Thirty-two F_1 (crossbred) rats, offspring of reciprocal matings between Wistar and DA rats. These F_1 rats were of similar appearance to the DA's i.e., pigmented agouties, but were distinguishable by patches of white fur on the legs and belly, due to the heterozygous form of the white spotting gene.

The rats were all male and aged between 60 and 70 days at the beginning of the experiment. Animals from each rat type were allocated randomly to each of the four tasks, with eight rats per type per task.

Housing consisted of racked small cages (36 x 26 x 20 cm) with wire mesh front and back and solid metal sides. Rats were housed two from the same group to a cage. The air-conditioned housing room was with a 12 light and 12 dark cycle.

Apparatus

The discrimination apparatus was one used previously for experiments on prior exposure and shape discrimination learning (Bell & Livesey, 1981). It comprised a small mesh cage (36 x 26 x 20 cm) joined along one of the longer sides to a wooden compartment (25 x 26 x 20 cm), which was painted flat grey. The compartments could be separated by a metal slide. A clear Plexiglass lid was hinged over each section. In the end of the wooden compartment opposite the cage section were two openings 9 x 9 cm, 4.5 cm apart. There were small food wells, one behind each opening. Backing onto each opening and hung from a metal rod was an aluminium panel (16 x 10 cm) on which each discriminative stimulus was displayed. The panels were held closed against the back of the openings by magnetic tape. A grey wooden shutter could be lowered in front of the cue panels.

All tasks involved a discrimination between an equilateral triangle (6.8 cm/side) and a circle of equal area (diameter 5 cm). For the VT task each shape was three dimensional, being 1 cm thick, and each was painted white on a black panel. For the 3DV tasks the stimuli were the same, but each shape was covered by a clear plastic plate (7.5 x 7 cm), so that the three dimensional shapes were clearly visible but could not be touched. The plastic plates were attached to the stimuli by white, double-

sided tape, which covered the surface of the shapes. For the TRV task shapes were the same as for VT and 3DV tasks but were white on white panels and the room lights were dimmed. For the three visual tasks the luminance reading in the discrimination area was 15.1 lux; but for this task it was reduced to 0.95 lux. For the 2DV task each cue was the same size as the 3D shapes, but was only two dimensional, being painted white on a black panel.

Procedure

The rats were placed on a restricted diet with water available *ad libitum* and were handled daily for six days before testing commenced. The rats were fed a set amount of food daily to maintain an appropriate level of motivation (at about 90% of *ad lib.* feeding body weight). As the albino and F₁ rats were heavier and ate more food *ad lib.* than did the DA rats, these two groups required slightly more food during the experiment to maintain a similar level of deprivation.

Pretraining. Each rat was placed in the discrimination apparatus and allowed to explore and eat from the food wells for fifteen minutes on each of two days. The reinforcement was minced, concentrated dog food (Loyal), shaped into small pellets. On the third day, each rat was taught to push the pretraining panels open (these were plain black) and to receive the food pellet from behind the panel. Each rat was required to complete 10 trials of panel push responses. If an animal adopted a position strategy (3 trials to one side) it was not rewarded for the next trial until it shifted its response to the other side.

Training. All rats were given 10 trials per day on their particular task with the position of the positive stimulus being varied according to Fellows' (1967) revision of the Gellerman sequence. A noncorrection procedure was used. If the rat responded incorrectly the shield was lowered immediately in front of the discriminative cue panels and the rat returned to the starting compartment ending the trial. An incorrect response was defined as a push on the panel with the negative cue. For a correct response, the rat pushed open the panel with the positive cue, and received a food pellet that was introduced from behind the panel on the end of a rod. To emphasise the negative cue in the initial learning trials, a wooden block was placed behind the negative panel for the first 30 trials. The block was positioned so that the panel would be blocked after opening only sufficiently to activate the negative response warning light. On later trials, when the animal pushed the negative panel, it swung open and then the experimenter closed it and the shield. This procedure was to prevent the rats from attempting to use the blocking of the panel as a pressure cue. If a rat scored 7/10 or better before complet-

ing 30 trials, the wood block was removed at that stage. Training was continued until a criterion of 90% correct responses over three consecutive days (27/30) was reached. Training was stopped at 300 trials if criterion was not attained. Two experimenters (the authors) trained the rats. For each task, half the rats were trained with the circle as the positive cue, the other half with triangle positive.

RESULTS

The main measure used was total number of errors (either to criterion or to 300 trials). This was preferred to the measure of number of trials to criterion because a number of albino rats failed to reach criterion. Progress in learning for each group is shown in Figure 1 in terms of mean percentage of correct responses for each successive block of 10 trials.

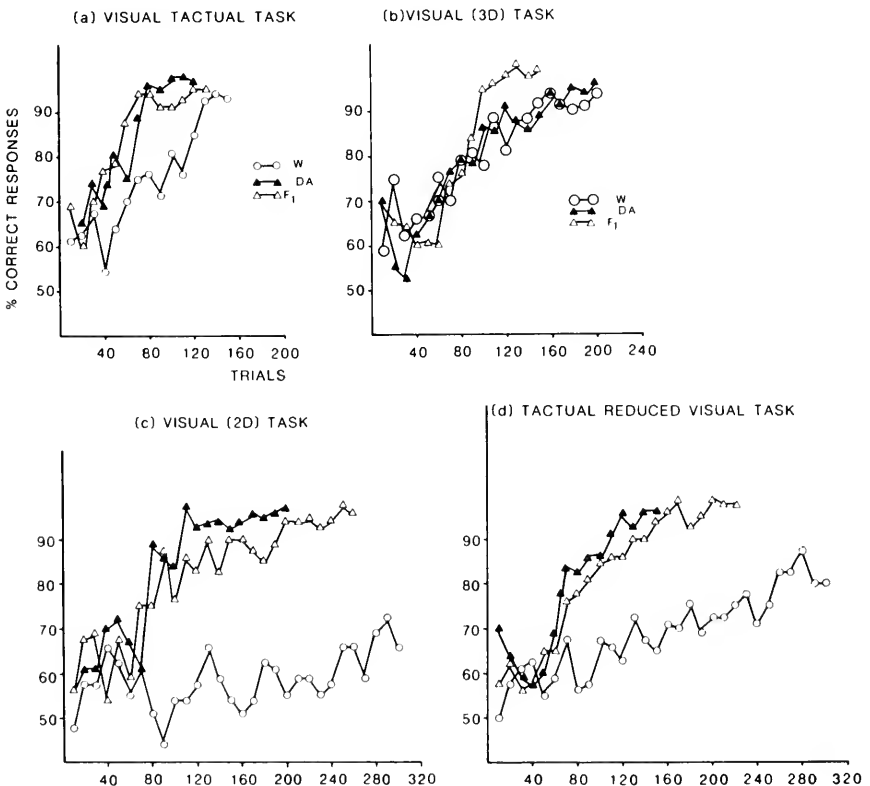


FIGURE 1. Mean percent correct responses for blocks of 10 discrimination trials for Albino Wistar (W), Pigmented DA (DA) and F1 rats on the four tasks; a. 3D Visual Tactual (VT). b. 3D Visual (3DV). c. 2D Visual (2DV). d. Tactual, Reduced Visual (TRV).

It is evident from the figure that there was little difference between W, DA and F₁ rats on the VT and 3DV tasks. However, on the 2DV and TRV tasks, the albino rats showed only slight improvement over the 300 trials whereas the pigmented animals learnt these tasks readily.

The analysis of errors confirmed these differences and also highlighted some more subtle differences. Figure 2 shows mean total errors for each rat type over the four tasks.

Analysis of variance revealed a significant rat factor, $F(2,84) = 47.18$, $p < .01$; a significant task factor, $F(3,84) = 21.62$, $p < .01$ and a significant interaction, $F(6,84) = 11.5$, $p < .01$. One way analyses were conducted

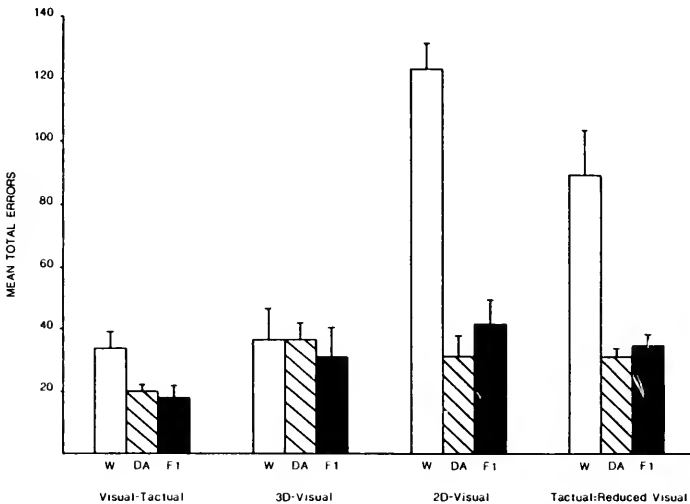


FIGURE 2. Mean total errors and standard errors for Albino Wistar (W), Pigmented DA (DA) and F₁ rats on the four tasks. a. 3D Visual Tactual (VT). b. 3D Visual (3DV). c. 2D Visual (2DV). d. Tactual, Reduced Visual (TRV).

within each factor to establish the basis for the interaction. For the rat analysis the significance level was set at .05/3 groups, i.e., .016 (Kirk, 1968). It was found that the rat stocks did not differ significantly in errors on the VT and 3DV tasks but there were significant differences on the 2DV task, $F(2,84) = 55.5$, $p < .01$; and on the TRV task, $F(2,84) = 23.3$, $p < .01$. As is evident in Figures 1 and 2, it was the W groups that performed poorly on these two tasks; with only one W rat reaching criterion on the 2DV task and three reaching criterion on the TRV task. All the pigmented rats reached criterion on these tasks. For the task analysis (significance level of .05/4 tasks, i.e., .0125), only for the albino rats was there a significant difference in errors between tasks, $F(3,84) = 40.8$, $p < .01$. On the TRV task the albino rats made significantly more errors than on the VT and 3DV tasks while, on the 2DV task, significantly more errors occurred than on the other three tasks.

Thus, for pigmented rats, all four tasks were of a similar level of difficulty, all being learnt readily. For the albino rats, performance on the VT and 3DV tasks was comparable with that of the pigmented animals but much more difficulty was experienced with the other two. The TRV task was significantly more difficult for the W rats, with the majority failing to reach criterion, while the 2DV task proved the most difficult.

Further information on the use of visual and tactual cues was gained from observation of rats during training on the VT and TRV tasks, where both cues were available. One experimenter recorded instances of unambiguous use of either visual or tactual cues on trials where a correct choice was made. A rat was recorded as using visual cues if the choice of stimulus was made well before it could make physical contact with the stimulus. Use of tactual cues was defined as contact with both shapes, usually by vibrissae, snout or mouth, before making a correct choice. A total of 8 W, 10 DA and 8 F_1 rats, over both tasks, were recorded as demonstrating unambiguous cue use. The other rats appeared to be using a mixture of cues on a particular trial, or it was not possible to ascertain what they were doing. For example, rats often made physical contact with one shape, then appeared to visually inspect the other before making a choice, responding to the first stimulus.

Table 1 shows proportions of rat groups using (a) visual cues only, (b) tactual cues only, (c) visual cues on some trials and tactual cues on others and (d) undetermined or ambiguous cue use.

Over both tasks, more of the albino rats used tactual cues, either alone or interspersed with visual cues, whereas the pigmented rats, particularly, the DAs, favoured the visual cues even on the TRV task. The F_1 rats' cue use fell between that of the two strains. The three W rats

TABLE 1
Proportions of Rat Groups Using Different Cues
While Learning the VT and TRV Tasks

RAT TASK	W		DA		F_1	
	VT	TRV	VT	TRV	VT	TRV
<i>Cue use:</i>						
a) Visual only	.125	0	.5	.25	.25	.125
b) Tactual only	0	.375	0	.125	0	.125
c) Visual and Tactual	.5	0	.25	.125	.375	.125
d) Ambiguous	.375	.625	.25	.5	.375	.625

which used tactual cues alone did not reach criterion. Thus the use of tactual cues alone did not appear to be a successful learning strategy although it appeared that many rats were successful with some combination of visual and tactual cues (see proportions of groups in categories c and d).

DISCUSSION

The results for two of the tasks were as predicted, with the Wistar rats learning the 3D Visual-Tactual task readily, but proving much less capable on the 2D Visual task. The results for the other two tasks were not expected, particularly with regard to the difficulty the Wistar rats experienced with the Tactual-Reduced-Visual task, for which it was thought that they would use the tactual cues to effect learning quite readily. The success of the Wistar rats on the 3D Visual task was also surprising in view of the reported superiority of the pigmented rats in visual acuity.

A study has demonstrated that there are a considerable number of binocular cells in the albino rat visual cortex, particularly around the border between areas 17 and 18a (Diao, Wang & Pu, 1983). The proportion of binocular cells was lower than in pigmented mice and hamsters; however, the proportion in the albino rat was higher than in other albino animals such as the Siamese cat. In the rat much of the binocular input appears to be from callosal fibres, which contribute input from the ipsi-lateral eye. Blakemore (1969) has suggested that such callosal input may be important for stereoscopic vision. Our finding that albino rats were able to make significantly better use of the 3D than the 2D visual cues is congruent with the proposition that they have some stereoscopic vision. Other cues not necessarily related to binocularity may also have increased the salience of the 3D cues (e.g. shadows).

Another outcome that was not anticipated was the relatively poor performance of the Wistar rats on the Tactual-Reduced Visual task. It was expected that the albinos would show greater reliance on tactual cues than pigmented rats and would thus be able to perform adequately on this task. Proportionately more of the Wistar rats did appear to try to use tactual cues but were not successful with this strategy. The response required in the task, i.e. a press on the panel bearing the cue, may well have adversely affected the performance of the tactual discrimination. From the observations recorded during training it appeared that when the rat contacted the panel to test the cue tactually it had difficulty inhibiting the press response when the incorrect panel was tested. With visual cues the inhibition of response to the cue could be spatially separated from the operant press response that followed contact with the panel. An equivalent separation of cue testing from operant response

would therefore seem necessary if a direct comparison is to be made of the efficacy of visual versus tactual cues.

A second problem, evident with the albinos particularly, was in the attention paid to an irrelevant cue, namely the pressure required to push open the stimulus panels. Rats appeared to attempt to assess which panel would open more easily, but of course such a strategy did not correlate in any way with the positive stimulus as there was no difference in the way the panels were held and in any case the correct panel varied from side to side at random. This appeared to interfere particularly with W rats' learning of the TRV and 2DV tasks. On these tasks, although the majority of the W rats did not reach criterion, some did show good performance on some days. On the 2DV task, besides the rat that reached criterion; three scored 9/10 at least once, three scored 8/10 at least once, and the other rat did not get beyond 7/10. On the TRV task, apart from the three rats that reached criterion, four scored 9/10 at least once, and the other, 8/10. The pattern on both tasks towards the end of training, for those rats which did not reach criterion, was for a good score on one or two days followed by one or more days with low scores. Thus the rats apparently were able to attend to and use the relevant cues on some days but had great difficulty in sustaining performance over a long enough period to reach criterion. They seemed to revert to using irrelevant cues, particularly the pressure required to open the panels. Therefore, as we had initially assumed, quite a number of W rats tried to use tactual cues but this was not a particularly effective strategy in this apparatus.

In this study the anticipated difference between albino and pigmented rats in the ability to use weak visual cues was evident; but there was no difference with stronger visual cues. This difference with the weak cues does not appear to be due to any strain differences other than those related to abnormalities of the albino visual system, as the F_1 pigmented rats performed similarly to the DA rats on initial task learning.

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INFLUENCE OF EVOLUTIONARY BIOLOGY IN THE EARLY DEVELOPMENT OF EXPERIMENTAL PSYCHOLOGY IN ARGENTINA (1891-1930)

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ABSTRACT: Argentina's first laboratory of experimental psychology was founded in 1891 by the educational psychologist Víctor Mercante. Other laboratories were then opened in several universities during the following forty years, giving rise to a considerable development of experimental psychology. The emphasis on experimentation was a common feature of psychology in many other countries, including some Latin American ones. However, Argentine psychology differed from that of other Spanish-speaking countries in the relatively important influence of evolutionary biology on the thinking of several of the most influential psychologists, including José Ingenieros, Horacio G. Piñero, Víctor Mercante, and Rodolfo Senet, whose ideas and work are described in this paper.

RESUMEN: El primer laboratorio argentino de psicología experimental fue creado en 1891 por el psicólogo educacional Víctor Mercante. Otros laboratorios fueron abiertos en varias universidades durante los siguientes cuarenta años, dando lugar a un considerable desarrollo de la psicología experimental. El énfasis en la experimentación fue un rasgo común de la psicología en muchos otros países, incluyendo algunos latinoamericanos. Sin embargo, la psicología argentina difirió de la de otros países de habla hispánica en la influencia relativamente importante de la biología evolutiva en muchos de sus más influyentes psicólogos, incluyendo a José Ingenieros, Horacio G. Piñero, Víctor Mercante, y Rodolfo Senet. Sus ideas y contribuciones se describen en este artículo.

An historical review of the antecedents and development of experimental psychology in Argentina, from the arrival of Europeans in the 16th Century to the present, suggests that experimentalism was the dominant view between 1891 and 1930 (Foradori, 1935; Ingenieros, 1919a; Papini, 1976, 1978, 1987; Papini & Mustaca, 1979). Several factors contributed to the dominance of experimental psychology, including first, the strong influence from European psychology which had started by that time to move toward an increasingly experimental position (i.e., Wilhelm Wundt, George Dumas, Theodule Ribot, Herbert Spencer, C. Lombroso, etc.); second, the impact of "transformism," that is, the theory of evolution from common ancestors, as developed by Jean-Baptiste Lamarck, Charles Darwin, Herbert Spencer, Ernest Haeckel, and others, which placed psychology into a closer contact with the natural sciences where observational and experimental methods were well established; and third, a local philosophical tradition that began early in the 19th

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century with Juan C. Lafinur (1797-1824), Manuel Fernández de Agüero (1772-1840), and Diego Alcorta (1801-1842). A brief description of this local tradition and of some of the main political and social factors characterizing Argentina's history during the last century, will be useful to set up the framework within which experimental psychology developed toward the end of the 19th Century.

The importance of Lafinur, Fernández de Agüero, and Alcorta lies in their rejection of traditional scholastic philosophy in favor of ideology, a French movement initiated by Etienne de Condillac, Pierre Cabanis, and Antoine Destutt de Tracy. In the present context, it is the emphasis on sensory experience as the source of human knowledge that was central to the ideologists. Lafinur was appointed as Professor of Philosophy at the Colegio de la Unión del Sur de Buenos Aires, where he lectured between 1819 and 1821. His rejection of traditional philosophical ideas was so extreme that he was finally expelled from the Colegio. This college became the basis for the foundation of the University of Buenos Aires in 1821. Lafinur was followed by Fernández de Agüero, who lectured on ideology from 1822 to 1827, and who was in turn followed by Diego Alcorta, also an ideologist, who remained in this position until his death in 1842. These three philosophers were not extremely original, as Torchia Estrada (1961) has shown. They should be properly considered as professors of philosophy. However, they had a profound effect in the cultural movement both during their time and toward the end of the century, when positivism was at its height. Particularly important was Fernández de Agüero's book *Principles of Ideology* (1940) in which he suggested, following Cabanis, that psychology should be based on the study of sensory processes and nerve function. These ideas, although not very original at that time, served to set up a tradition that was later to influence some of the proponents of experimental psychology (e.g., Ingenieros, 1919a).

There were several political and social factors that undoubtedly influenced the emergence of experimental psychology. Between 1860 and 1930, Argentina's political system was relatively stable, and the country's economy, based on agriculture, was growing. Two aspects of the social life are perhaps of importance in relation to the expansion of universities: the relatively large educational investment based on the principle of equal opportunity for access to a free, non-religious system and on European culture, and the large immigration of people from several European countries, mainly Italy, which further strengthened the contact between Argentina and Europe. The new nation that was emerging out of internal conflicts was modeled from the ideas of Juan B. Alberdi (1810-1884) and Domingo F. Sarmiento (1811-1888). Alberdi played an important role in the political organization of the nation, whereas Sarmiento set up the basis for Argentina's educational projects. Both were pragmatic and both saw science as a main route for social

progress. Their ideas were so close to what was to be known as positivism, that it has been suggested that they actually developed an autochthonous Argentine positivism (Korn, 1949; Romero, 1952). Sarmiento was responsible for a number of projects about education that he carried out in his several public positions. During his presidential period (1868-1874), the universities expanded and several research institutes were created, such as the astronomical observatory of Córdoba (Babini, 1963). Argentina was rapidly growing and needed an effective educational system based on the particular features of its increasingly heterogeneous population. In addition, the influence of positivism naturally encouraged an empirical approach to education, and psychology benefited from this state of affairs. Wundt's experimental approach to psychology had a broad influence in Europe, the United States, and some Latin American countries, but the influence of evolutionary biology on psychology was far less impressive and general, particularly in Spanish-speaking countries (Ardila, 1982, 1987; Foradori, 1954). In this connection, however, Argentine psychology was an exception.

In this paper I describe some features of the early historical development of experimental psychology in Argentina. I concentrate on some of the psychologists who developed their activities at the Universities of Buenos Aires (founded in 1821) and La Plata (founded in 1897) not because these were the only Universities where experimental psychology was dominant (see Papini, 1976), but rather because of their wider influence in both academic and cultural activities and the discussion of social issues such as elementary education and mental health.

In 1891, Víctor Mercante (1870-1934) set up a small laboratory in a secondary school at San Juan, to study the psychology of children and apply this knowledge to improve educational practices. His main research topics concerned the development of reading and writing abilities, and the use of mental tests as research tools. Notice that Mercante's laboratory was founded only twelve years after Wundt's. Experimental laboratories were soon opened in other schools and universities, giving rise to a period of rapid growth and development of experimental psychology (Papini, 1976).

Mercante continued his research at the University of La Plata in 1906, with his main colleague, Rodolfo Senet (1872-1938). They set up a laboratory for the study of psychological functions in children with direct implications for education. Mercante and Senet carried out an extensive research project which emphasized the study of large samples of children and the use of statistical methods to describe the results and reach scientific conclusions. Mercante published *Psicología de la Aptitud Matemática [Psychology of Mathematical Skills]* in 1904, and *La Crisis de la Pubertad y sus Consecuencias Pedagógicas [The Crisis of Puberty and its Educational Consequences]* in 1918, with an extensive review of original research. In a similar vein, Senet published

his book *Elementos de Psicología Infantil [Elements of Child Psychology]* in 1911. Although Mercante and Senet were applied researchers, they believed that psychology should be based in evolutionary biology. For example, Mercante began his book on the crisis of puberty with a review of psychological development in animals, and pointed out that: "Survival is but a need to protect the offspring in the best possible way, against all kinds of risks and, in turn, to prepare it for the sexual act" (Mercante, 1918, p. 20). Mercante believed that the crisis of puberty was not exclusively observed in humans, but common to the reproductive stage of development of many species.

Moreover, Mercante and Senet placed a major emphasis on physical anthropology and neurobiology. They developed an extensive series of studies on the relationship between mental evolution and cephalic indices, and wrote about current theories of human evolution (cf. Mercante, 1918, pp. 55-99; Senet, 1909).

Between 1898 and 1901, Horacio G. Piñero (1869-1919) set up a laboratory at the University of Buenos Aires with equipment acquired in Germany (in 1901) and France (in 1902). The first university course in experimental psychology, with laboratory exercises, was then offered in 1901 by Piñero. The course emphasized the anatomical and physiological basis of emotions, attention, perception, memory, thinking, and language. Students had to carry out a research project as a complement to the course. In 1916 Piñero edited a two-volume book containing most of the research carried out by the group. The volumes were entitled *Trabajos de Psicología Normal y Patológica [Works on Normal and Pathological Psychology]*. The research carried out between 1905 and 1914, and published in the first volume of these Works, included 50 papers on topics such as memory (15 papers), attention (17), psychophysiology (11), and perception and psychophysics (7).

Piñero's view of experimental psychology was largely based on the biological sciences and on the Darwinian hypothesis of psychological continuity between species:

Experimental psychology does not exclusively mean laboratory psychology, but natural, objective psychology, with experience, observation, and study of the life and habits of animals and man, isolated and in groups. (Piñero, 1916, p. 10.)

It seems that Piñero's course attracted the attention of many students who were interested in the "new" experimental psychology. The University then decided to offer a second course. Felix Krueger, one of Wundt's disciples, moved to the University of Buenos Aires to teach this second course in 1906. Piñero's course was then oriented toward the experimental, physiological, and clinical aspects of psychology, whereas Krueger's dealt with higher mental functions and the relationship between psychology, philosophy, and the social sciences. Krueger

returned to Germany in 1909 and the course was offered by José Ingenieros (1877–1925), perhaps the most influential Argentine psychologist during this period, who had been appointed as Professor of Experimental Psychology in 1908. Krueger's presence was not an isolated event; many European psychologists lectured at the University of Buenos Aires during the period between 1900 and 1930, such as George Dumas, Pierre Janet, Stanley Hall, and Wolfgang Kohler.

Ingenieros was not a laboratory scientist but a philosopher with broad interests in the natural sciences (Lipp, 1969). His book on psychology, published in 1911 and entitled *Psicología Genética* [*Genetic Psychology*], was the result of a series of articles he wrote during 1910 for the medical journal *Argentina Médica*. This book was later published in Spain and France as *Principios de Psicología Biológica* [*Principles of Biological Psychology*] in 1913, and in Germany and Argentina as *Principios de Psicología* [*Principles of Psychology*] (Ingenieros, 1919b).

Ingenieros was deeply influenced by Darwin's theory of evolution and by Spencer's idea of evolutionary progress. His *Principios* shows the extent to which he integrated evolutionary thinking and psychology. Ingenieros extended the idea of evolution from phylogeny to the individual organism (ontogeny), and to human societies (sociogeny):

Psychology studies the *natural formation of psychological functions* in the evolution of living species, in the evolution of human societies, and in the evolution of individuals. (Ingenieros, 1919b, p. 9.)

According to Ingenieros, psychological functions are adaptive reactions of organisms to environmental conditions; they evolve as any other biological character through the action of natural and sexual selection and through the inheritance of acquired skills. He conceptualized psychology as a branch of the biological sciences whose object of study was the development of psychological functions in individual organisms (Ingenieros, 1919b, pp. 323–324). Ingenieros was concerned about the lack of interest in evolutionary biology shown by psychologists of his time, and placed a major emphasis on comparative psychology as a basic substrate of psychology as a whole (Papini, 1985).

Ingenieros realized that non-human animals could not be studied by the classic subjective methods, and suggested that comparative psychologists should measure the behavior of organisms as an objective assessment of psychological functions:

The *psychological phylogeny* can only be reconstructed through the observation of the behavior of living beings, that is, by studying the means of expression of their psychological functions. (Ingenieros, 1919b, p. 301.)

Ingenieros went on to point out that objective observation was the main tool for studying not only the comparative, but also the develop-

mental and social roots of mental capabilities. Introspection was not a useful technique when studying infants or adults from "primitive" societies. His emphasis on behavior and on objective methods is not original, but it does not seem to have been developed out of behaviorism since there is no reference to J. B. Watson even in the last edition of his *Principios* (Ingenieros, 1919b). Ardila (1982) suggested that Ingenieros was the first Latin American psychologist who proposed an original and coherent conceptualization of psychology, one based on evolutionary principles and which he called "genetic psychology."

Neurobiology, in Argentina, was developed by the German scientist Christofredo Jakob (1866-1956), who arrived in the country in 1899 hired by the University of Buenos Aires as director of the Clinical Psychiatric Laboratory. His main research projects were carried out in the Neuropsychiatric Hospital in Buenos Aires, where he was appointed as director of the Laboratory of Neurology in 1912. He also held faculty positions at the Universities of La Plata (between 1922 and 1933) and Buenos Aires (between 1913 and 1944).

Jakob was interested in the evolution of the brain in general and of the cerebral cortex in particular. His approach to these topics was exclusively neuroanatomical and it was based on the study of species from the Argentine fauna. Jakob summarized his contributions in a series of volumes entitled *Folia Neurobiologica Argentina*. Some of these volumes dealt with topics such as the human brain, the frontal lobe, and the origin of the neocortex, whereas others described the neurobiology of some species typical of the Argentine fauna. For instance, his theory of the phylogenetic origin of the neocortex was based on a series of histological studies on the brain hemispheres of a small apod reptile, *Amphisbaena* (Jakob, 1945).

In collaboration with Clemente Onelli (1864-1924), an Italian scientist also working in Argentina, Jakob published in 1913 the *Atlas del Cerebro de los Mamíferos de la República Argentina* [*Atlas of the Brain of Argentine Mammals*], in which they intended to establish the biological basis of psychological phenomena. Jakob and Onelli (1913) pointed out that the comparative study of the structure and function of the central nervous system would eventually explain psychological phenomena; otherwise, psychology would be limited to the descriptive method.

There were several empirical studies on comparative psychology during this period, most of which can be characterized as anecdotal observations of the behavior of several species. Examples of these studies are Onelli's (1905) observations on the reproductive behavior of *Rhea americana*, including the role of males in parental care, and Fonticelli's (1905) observations on the behavior of Southern sea lions. There was also some interest in the intellectual capacities of animals in general (Kermes, 1893), and of monkeys in particular (Holmberg, 1893).

Unfortunately, none of these works developed into a coherent research program.

During the initial two decades of this century, experimental psychologists were in close intellectual contact with a group of paleontologists from the University of La Plata. The leader of this group was Florentino Ameghino (1854-1911), who is best known because of his studies and theories on the origin of mammals and on human origins. Ameghino's ideas were extensively described by some of the experimental psychologists such as Ingenieros (1956) and Senet (1909). Ameghino himself published a review of his results in a volume of the *Anales de Psicología* [*Annals of Psychology*] (Ameghino, 1910) and was a member of the Buenos Aires Society of Psychology, founded in 1908 by Ingenieros, Piñero, Mercante, and others.

In conclusion, the leading Argentine experimental psychologists of this period were all influenced by evolutionary biology. They firmly believed that psychology could achieve a scientific level if it could be established on the basis of evolutionary biology and the experimental method. This was not only a theoretical conceptualization of a discipline, but also served as a fundamental step toward the solution of the social problems of that period. For example, the educational endeavors of President Sarmiento were an important source of inspiration for these psychologists. Their contribution to the success of the educational program was the idea that it must be developed on the basis of the characteristics of Argentine children, and that these could best be determined by an empirically oriented experimental psychology that was developmental and biologically, i.e., evolutionarily, based.

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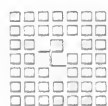
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